THE THALAMUS AND ITS CORTICAL PROJECTION IN THE BRUSH-TAILED POSSUM, TRICHOSURUS VULPECULA, AND THE NATIVE CAT DASYURUS VIVERRINUS, WITH A COMPARATIVE REVIEW OF THALAMIC ORGANISATION IN MARSUPIAL AND PLACENTAL MAMMALS

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This thesis contains no material which has been accepted for the award of any other higher degree or graduate diploma in any university, and to the best of my knowledge and belief contains no material previously published or written by another person except when due reference has been made in the text.

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ABSTRACT

This thesis is presented in two parts:

The first comprises a review of thalamic structure and connections in marsupial mammals, and comparison with placental species.

The major groups of thalamic nuclei are treated in turn. The cytoarchitecture of each group is described and compared in different marsupials, with greatest emphasis being placed on the Virginia opossum Didelphis virginiana, the brush-tailed possum Trichosurus vulpecula, and the native cat Dasyurus viverrinus. The presently available information on afferent and efferent connections of specific regions in marsupials and placentals is then reviewed, and comparisons made within and between the two mammalian groups. Possible functional roles of each region are also briefly discussed.

Among marsupials many fundamental similarities in thalamic organisation are evident, but also several important differences. Most of these differences can be seen to be related to particular groupings of animals, or to follow trends across the range of species examined. Representative Australian

diprotodonts, such as Trichosurus, and to a lesser extent polyprotodonts, such as Dasyurus, exhibit a number of features which distinguish them from the American didelphids, such as the opossum Didelphis. Most of these variations in thalamic organisation show clear parallels to the morphological and serological distinctions between the three marsupial groups. Some of the distinguishing characteristics of Australian forms represent considerable progress from the relatively primitive level of development found in the didelphids, and convergence upon the more highly evolved organisational plans of advanced placental mammals.

Comparisons of the connective relationship of specific thalamic regions in marsupials and placentals reveal many features which are shared by most or all species. There are occasional significant departures from what apparently constitute general mammalian plans, however most cases where important interspecies variations occur concern details in the distribution patterns of particular input and/or output connections.

The most marked differences in connection patterns among both marsupials and placentals are found with the rostral ventral tier nuclei (ventroanterior-ventrolateral complexes and ventromedial nucleus or possible equivalent) and the central intralaminar

group. Most other thalamic centres appear to have rather more uniform organisation.

The second part of the thesis comprises published details of examinations of thalamic and cortical structure and connections in the brush-tailed possum Trichosurus vulpecula, and the native cat Dasyurus viverrinus, with short notes on somatosensory cortical organisation in the rufous wallaby Thylogale billardierii.

INTRODUCTION

The Virginia opossum, Didelphis virginiana has attracted considerable attention from workers in the field of comparative neurobiology, and has played an important part in our understanding of evolutionary processes in the mammalian central nervous system. Its popularity as a research animal is due in large part to its relatively undifferentiated brain, as well as to its ready availability and general convenience for experimental manipulations. These factors until recently made Didelphis by far the most extensively studied of all 'primitive' mammals. Most work has concentrated on examination of the organisations of sensory and motor systems. The degree of advancement of certain aspects of these systems in other species have frequently been measured against a Didelphis 'baseline'.

Among marsupials Didelphis takes on even greater significance, in that it is representative of the family Didelphidae, the stem marsupial group, and may thus be considered to be a model of the ancestral polyprotodont line from which other, including Australian, marsupials are derived (Kirsch 1977).

Lende (1963a, b) in his electrophysiological mapping

studies of the Didelphis neocortex, found that in this animal the somatic sensory and motor areas are fully overlapping and congruent. His results have since been substantiated by a similar physiological study in another species of didelphid opossum (Magalhaes-Castro and Saraiva 1971), and by anatomical evidence that the cortical projections of the ventroposterior (VP-somatic sensory relay) and ventroanterior-ventrolateral (VA-VL-motor relay) thalamic nuclei overlap extensively if not completely in Didelphis (Donoghue and Ebner 1981a, Killackey and Ebner 1973).

Lende (1963c) applied the same mapping procedures in an Australian marsupial, the wallaby Macropus (= Thylogale) eugenii, and obtained results very similar to those in Didelphis. In comparing his findings in these two marsupials with those of similar studies in other species he concluded that a significant degree of somatosensory and motor functional overlap in the cortex constitutes a relatively primitive level of organisation, while the processes of evolution in more advanced animals have favoured functional separation (Lende 1969).

Wallabies are members of the derived order Diprotodonta, which also includes kangaroos, possums and wombats. Some of these animals, and in particular the more advanced macropods (kangaroos and wallabies)

show a high degree of morphological specialisation. Serological evidence indicates that while members of this order are closely related to each other, the group as a whole has diverged considerably from the stem polyprotodont line, as represented by the Didephidae, and that this divergence probably began soon after the separation of the American and Australian populations (Kirsch 1977).

The close parallels between Lende's findings in two such distantly related species,then,provided a strong case for assuming that the organisations of the somatosensory and motor systems were probably very similar in all marsupials, and that this organisation had remained at a relatively primitive level.

On the other hand,however,a body of evidence from work carried out both prior and subsequent to that of Lende suggested that at least some Australian marsupials may not follow the Didelphis plan. Studies in a number of polyprotodont and diprotodont species (including some wallabies) showed that low intensity electrical stimulation of only rostral and medial parts of the parietofrontal or sensorimotor cortex produces discrete body movements (Abbie 1940, Goldby 1939, Rees and Hore 1970). In contrast, the area of cortex responsive to somesthetic stimulation in representative

diprotodonts is relatively extensive, but does not include the extreme rostromedial margin of the parietofrontal area (wombat, Johnson et al 1973; Tasmanian pademelon, Weller et al 1976, 1977; brush-tailed possum, Adey and Kerr 1954, Haight and Weller 1973, Weller and Haight 1973 plus unpublished observations). This region was shown by the anatomical studies of Ward and Watson (1973) in the brush-tailed possum Trichosurus vulpecula to receive projections from the ventrolateral thalamic nucleus.

Comparison of the findings of these different studies would suggest that a significant degree of separation of somesthetic and motor functions may be present in the cortices of at least some Australian species, such that caudolateral parts of the parietofrontal area may be primarily or exclusively sensory, and a small rostromedial zone primarily or exclusively motor, with a region of functional overlap in between.

Such an organisation would represent a considerable advance from the Didelphis - like arrangement attributed by Lende to the wallaby, and by inference to other Australian forms, and invites comparison with placental species such as the rat, in which the sensory and motor cortical areas overlap only partially (Hall and Lindholm 1974).

In order to resolve this confict between the results of Lende and other workers, it was decided to obtain an anatomical measure of the extent of overlap of the somatosensory and motor cortical areas in a representative Australian marsupial, by delineating the projection fields of the ventroposterior (VP) and ventrolateral (VL) thalamic nuclei.

The retrograde horseradish peroxidase (HRP) labelling method (LaVail et al 1973) offered a rapid, simple and reliable method of displaying thalamocortical relationships. The brush-tailed possum Trichosurus vulpecula was selected as the most suitable experimental animal, due in part to its status as a relatively generalised representative of the diprotodonts, in part to its ready availability and convenient size, and not least to the existence of a respectable amount of information on thalamic and cortical structure, function and connections in this animal (Abbie 1940, Goldby 1939, 1941, 1943, Haight and Weller 1973, Hayhow 1967, Packer 1941, Rees and Hore 1970, Rockel et al 1972, Weller and Haight 1973).

Preliminary results (Haight and Neylon 1977a) showed that,in distinct contrast to the Didelphis organisation (Killackey and Ebner 1973), the VP and VL cortical projection fields in Trichosurus showed a relatively

limited area of overlap. The location and extent of these fields was also found to correspond reasonably closely to those of the somatosensory and motor areas respectively, as delineated by electrophysiological methods in this and other diprotodonts (see above).

Thus, both anatomical and physiological evidence was available which contradicted Lende's (1963c) findings in the wallaby, and which suggested that Trichosurus, and possibly other Australian species, possess a relatively advanced organisation of the somatosensory motor cortical areas, comparable in general terms to that seen in more advanced placental species, and in particular the rat (Hall and Lindholm 1974).

Various other factors also pointed to the Trichosurus brain being more advanced in certain respects than that of Didelphis. Goldby (1941), in his description of the Trichosurus thalamus, reported that the VP and VA-VL nuclear complexes contained clearly delineated cytoarchitectural subdivisions, which Rockel et al (1972) later showed to be closely related to the terminal fields of particular somesthetic and motor pathways. In Didelphis, on the other hand, the terminal fields of these same pathways (Hazlett et al 1972, Walsh and Ebner 1973) could not be related to cytoarchitecturally distinct areas within the VP and VA-VL complexes (Bodian 1939, Oswaldo-Cruz and Rocha-

Miranda 1967). Hence, in Trichosurus the ventral tier nuclei could be considered to display a higher level of differentiation than those of Didelphis.

Furthermore, Hayhow (1967), whose results were later confirmed by Rockel et al (1972), observed that in Trichosurus the principal visual relay centre of the thalamus, the dorsal lateral geniculate nucleus (LGd), has a rather complex cellular organisation, and still more complex pattern of retinal inputs. In contrast the LGd of Didelphis and another species of American opossum were shown to have relatively simple organisations, in terms of both cytoarchitecture and the arrangements of retinal projections (Lent et al 1976, Royce et al 1976, Oswaldo-Cruz and Rocha-Miranda 1967).

It seemed clear from these findings that Trichosurus showed important differences to Didelphis with respect to thalamic and cortical organisation. In addition, our preliminary investigations of thalamocortical connections in Trichosurus had produced results which suggested that there may be significant differences between the relationships of some other thalamic centres in this animal, and similarly located and named regions in other species (Haight and Neylon 1977b, Neylon and Haight 1977). We had also noted an unusual degree of morphological variation within the thalamus

and neocortex in our Trichosurus population (Haight and Neylon 1977c and (at that time) unpublished observations). These various factors clearly warranted further investigation.

The scope of the Trichosurus study was therefore expanded to encompass a detailed examination of overall thalamic structure, and of the thalamic relationships of different regions of the neocortex (see fig 1). The results of these investigations have demonstrated that, while Trichosurus shows many similarities to Didelphis and to certain placental animals, it also shows a number of significant organisational differences (Haight and Neylon 1978a,b,c, 1979, Haight et al 1980, 1983, Neylon and Haight 1983).

Concurrently with the Trichosurus study a more limited examination was undertaken in the native cat Dasyurus viverrinus, of the general cellular organisation of the thalamus and of thalamic projections to parietofrontal cortex. This was done to determine whether a representative Australian polyprotodont marsupial, a group whose members morphologically and serologically more closely resembles American forms than the diprotodonts (Kirsch 1977), showed greater similarity to its fellow Australian, Trichosurus, or its co-ordinor Didelphis. Our results indicate something of a blend of Trichosurus and Didelphis characteristics, but

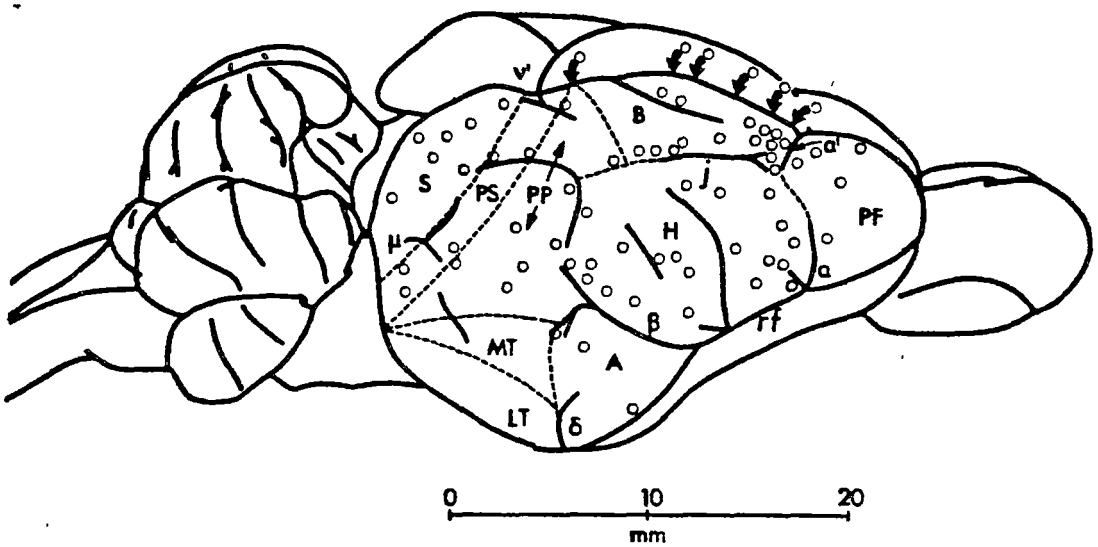


Figure 1

Lateral view of the Trichosurus brain showing locations of cortical horseradish peroxidase (HRP) injections which resulted in retrograde labelling of thalamic neurons. Individual penetration sites indicated by circles. Arrows indicate injections made into the extreme medial margin of the neocortical mantle. (For details of experimental procedures see Haight and Neylon 1978b, Haight et al 1980, Neylon and Haight 1983). Broken lines indicate boundaries of the main cortical cytoarchitectural zones, each denoted by capital letters. A - auditory cortex, B and H - body and head regions of sensory motor cortex, LT and MT - lateral and medial temporal areas, PF - prefrontal area, PP - posterior parietal area, PS - peristriate area, S - striate area. (For details of cortical cytoarchitecture see Haight et al 1980, Neylon and Haight 1983). Constant landmark sulci indicated by Greek symbols and lower case letters. j - jugular sulcus, rf - rhinal fissure.

show that in important respects Dasyurus is more comparable to Trichosurus (Haight and Neylon 1981a,b).

Since the completion of much of this work, and the publication of some of our results, a number of studies have provided further information on thalamic organisation and connections in Didelphis and other marsupials, and in placental animals, enabling more meaningful comparisons to be made between our own and other's findings. The main part of this thesis will therefore take the form of a summary and comparative review of what is presently known about the structure and connections of the thalamus in marsupials, and relate the various findings for this group to aspects of thalamic and cortical organisation in placental species.

In addition to this, a second part will comprise the published details of our examinations of thalamic cytoarchitecture in Trichosurus and Dasyurus, of the neocortical relationships of specific nuclei or nuclear groups in these animals, and of morphological variations found in the thalamus and neocortex in our Trichosurus population.

PART 1

REVIEW OF THALAMIC STRUCTURE AND CONNECTIONS IN MARSUPIALS AND COMPARISON WITH PLACENTAL SPECIES

In the following review the principal groups of thalamic nuclei will be considered in turn. Each group will be treated as follows:

Firstly, the cellular organisation of each region will be described and compared in those marsupial species for which most information is available. For the most part discussion will be limited to *Didelphis*, *Trichosurus* and *Dasyurus*, since these animals have been examined in greatest detail. In some cases relevant findings in other species will also be considered.

Descriptions of specific regions in *Didelphis* will be based mainly on information from the studies of Bodian (1941) and Oswaldo-Cruz and Rocha-Miranda (1967), as well as on examination of material available in this laboratory. The general organisation of the *Trichosurus* thalamus has been described by Goldby (1941) and ourselves (Haight and Neylon 1978a), while selected areas have undergone more detailed examination (Aitkin and Gates 1983, Haight and Neylon 1978c, 1979,

Hayhow 1967, Neylon and Haight 1983, Rockel et al 1972). We have also presented an analysis of thalamic structure in Dasyurus (Haight and Neylon 1981a). Observations on the cytoarchitecture of selected thalamic regions in other marsupial species will be based mainly on examination of material available in this laboratory.

The principle points of similarity between different animals will be briefly outlined. More detailed discussion will be presented where interspecies variation is apparent, and where there are differences or difficulties in nomenclature or treatment of particular regions in different studies. In some cases comparisons may be made between selected thalamic centres in marsupials, and possible homologous regions in placental animals.

Following each discussion of nuclear structure, the available information on connections of the constituents of each group of nuclei will be reviewed and comparisons made among different mammals. Since in general more is known of the neuroanatomical relationships of particular regions in placental animals these will in most cases be treated first to provide a basis for comparison with data obtained in marsupials. For the most part subcortical afferent connections and cortical relationships, or alternately

afferent and efferent connections, will be examined separately. Information related to the possible functional roles of each nucleus or region will also be presented and discussed.

MIDLINE AND CENTRAL INTRALAMINAR NUCLEI

In the following discussion the term 'midline group' will refer to the paraventricular, reunient, subparataenial and intermediodorsal nuclei. The term 'central intralaminar nuclei' (CIN) will refer to the central, paracentral, centrolateral, parafascicular, centromedian, rhomboid and interanterodorsal nuclei. The rhomboid and interanterodorsal nuclei have been included in the CIN on the basis of experimental findings in Didelphis (Hazlett and Bagley 1983) and Dasyurus (Haight and Neylon 1981b).

1. DESCRIPTIONS AND COMPARISONS OF NUCLEAR STRUCTURE IN MARSUPIALS

In terms of relative size and internal complexity, as defined by the number of discrete nuclei present, the midline and central intralaminar complexes are a very pronounced feature of the Didelphis thalamus (Bodian 1939, Oswaldo-Cruz and Rocha-Miranda 1967), somewhat less so in Dasyurus (Haight and Neylon 1981a), and considerably less so in Trichosurus (Haight and Neylon 1978a). Apart from this variation in the degree of development and internal subdivision, and some differences in the nomenclature applied to the American and Australian species, it would appear that the nuclei

are similarly organised in the three animals.

(a) SOME PROBLEM AREAS

The nuclei designated "parafascicular" and "posterolateral parafascicular" by Bodian (1939) and Oswaldo-Cruz and Rocha-Miranda (1967) in Didelphis correspond to the centrolateral and parafascicular nuclei respectively of Dasyurus and Trichosurus (Haight and Neylon 1978a, 1981a), as well as other species (see Mehler 1969). Examination of Didelphis material available in this laboratory showed that these nuclei are essentially similar in the three marsupials. The nomenclature has been standardised accordingly.

Another major problem concerns the status of the interanterodorsal nucleus (IAD). Earlier investigators have placed this nucleus with the anterior group nuclei, generally referring to it as a "commissural" nucleus associated with the anterodorsal nucleus (Goldby 1941 in Trichosurus, Bodian 1939, and Oswaldo-Cruz and Rocha-Miranda 1967, in Didelphis). In our description of the Trichosurus thalamus (Haight and Neylon 1978a) we also treated IAD with the anterior group.

Our experimental results in Dasyurus, which demonstrated a neocortical projection from IAD (Haight

and Neylon 1981b), together with recent evidence for a projection to the striatum in Didelphis (Hazlett and Bagley 1983), now raise the possibility that this nucleus could be part of the CIN group. Against this is our failure to demonstrate a neocortical projection for IAD in Trichosurus, and the fact that IAD appears not to receive connections from any of the major fibre systems terminating in other CIN nuclei (see below). Nonetheless, IAD does lie within the internal medullary lamina, and it is cytoarchitecturally very similar in the marsupials so far examined. On the basis of location we feel that IAD is better placed with the midline and central intralaminar groups and more specifically suggest that it may belong to the CIN.

(b) CENTRAL INTRALAMINAR NUCLEI

(For illustrations see Haight and Neylon 1978a figs 3-9, Haight and Neylon 1981a figs 2-10, Oswaldo Cruz and Rocha-Miranda 1967 figs 4-12).

The rhomboid (RH) and central (C) nuclei lie in the midline. In the two polyprotodont marsupials RH and C are clearly separated (Haight and Neylon 1981a, Oswaldo-Cruz and Rocha-Miranda 1967), while in Trichosurus the rhomboid nucleus cannot be distinguished (Goldby 1941, Haight and Neylon 1978a).

In Didelphis and Dasyurus RH is limited to the rostral half of the interthalamic adhesion, and extends somewhat more rostrally than C. In all species C is found throughout most of the extent of the interthalamic adhesion. Cytoarchitecturally, RH and C are similar, except that the cells of RH are less densely packed.

Extending laterally from the central and rhomboid nuclei, and contained within the fibres of the internal medullary lamina (iml), are three CIN nuclei. The interanterodorsal nucleus is small but distinctive due to the tight packing of its cells. It occupies the most rostral portion of the iml. The paracentral nucleus (PC) and the centrolateral nucleus (CL) replace IAD caudally, and extend through all but the most caudal portions of the iml. CL is located dorsolateral to PC. Rostrally, these nuclei are relatively distinct structures, however at more caudal levels their constituent cells are less closely packed, making it more difficult to distinguish boundaries with adjacent nuclei.

Caudally, the paracentral and centrolateral nuclei are eventually replaced by the parafascicular nucleus (PF), which is characterised by the close packing and dense staining of its cells. Throughout most of its extent PF is found in association with the fibres of the

habenulointerpeduncular tract. There is no evidence for separation of a distinct centromedian nucleus from the parafascicular nucleus. Such separation is apparently characteristic only of certain placental species (see Mehler 1966).

(c) MIDLINE NUCLEI

(For illustrations see Haight and Neylon 1978a figs 2-8, Haight and Neylon 1981a figs 2-9, Oswaldo-Cruz and Rocha-Miranda figs 3-11).

The remaining nuclei belong to the midline group, the most prominent of these being the paraventricular nucleus (PV). This nucleus is found throughout the dorsal part of the interthalamic adhesion, and merges caudally with the periaquaductal grey of the midbrain. In Dasyurus and Trichosurus the paraventricular nucleus differs from that of Didelphis. In Didelphis the midline and immediate periventricular zone remain cell sparse throughout the interthalamic adhesion. In Trichosurus this region is filled by a darkly staining, compact median seam of cells which is present throughout the entire extent of the adhesion. In Dasyurus this seam is not present rostrally, and in this region the paraventricular nucleus resembles that of Didelphis. However, the seam appears eventually,

and from that point caudad, the Dasyurus PV resembles that of Trichosurus. In Didelphis the paraventricular nucleus has been divided into distinct anterior (rostral) and posterior (caudal) subdivisions (Bodian 1939, Oswaldo-Cruz and Rocha-Miranda 1967). Because of the continuity afforded by the median seam in Dasyurus and Trichosurus such a separation is not apparent in these animals.

The subparataenial (SPT) and reunient (RU) nuclei are similar in Didelphis and Dasyurus. In these animals SPT first appears rostral to the interthalamic adhesion, inferior to the paraventricular and parataenial nuclei. With the appearance of the adhesion the two nuclei meet, but do not quite join on the midline. With the appearance of the CIN the SPT separates from the paraventricular nucleus and comes to lie below the CIN. The small reunient nucleus then appears below SPT. Caudally, SPT continues to decrease in size and is eventually replaced by the submedius nuclei on either side. RU remains small throughout its extent.

In agreement with Goldby (1941), we have not separated SPT and RU in Trichosurus (Haight and Neylon, 1978a). The Trichosurus reunient (reunient-subparataenial) nucleus remains quite large and distinct along the entire ventral margin of the interthalamic adhesion.

Finally, interposed between the paraventricular and the rhomboid nuclei in Didelphis is a large, but rather ill-defined cell mass, which has been termed the intermediodorsal nucleus by Bodian (1939) and Oswaldo-Cruz and Rocha-Miranda (1967. This nucleus is not present in either of the Australian forms though its presence is confirmed in Didelphis.

2. CONNECTIONS AND FUNCTIONS OF THE MIDLINE AND CENTRAL INTRALAMINAR NUCLEI

(a) CENTRAL INTRALAMINAR NUCLEI

(i) SUBCORTICAL AFFERENT CONNECTIONS

Placentals

Numerous studies in placental animals have demonstrated inputs to the CIN from a variety of subcortical centres. Connections from some sources encompass several CIN divisions, while others are directed primarily or solely to specific nuclei.

In the rat the cerebellum projects strongly to the CIN, but principally to CL and PF (Donoghue et al 1979, Faull and Carman 1978, Haroian et al 1981). In the cat, where the centromedian nucleus (CM) and PF are distinctly separate cytoarchitectural entities, PF does

not receive substantial cerebellar connections, however CM and the remaining CIN divisions do (Hendry et al 1979, Sugimoto et al 1981). Monkey cerebellar connections probably do not terminate in either CM or PF, but connect primarily to CL and PC (Chan-Palay 1977, Kalil 1981).

There is general agreement then that CL is an important thalamic recipient of cerebellar connections, with PC and perhaps C being of lesser importance. The apparent variations found in cerebellar connections with PF and CM in different animals may in part be due to differences in the sensitivity of tracing techniques, or more probably in the differentiation by different workers between supposed cerebellar terminal fields in these nuclei, and fibres passing through them (see Chan-Palay 1977). It is possible, however, that they represent genuine species differences.

There is greater interstudy consensus with respect to superior collicular and spinal connections with the CIN. In the cat and monkey the deeper collicular layers have widespread projections to the CIN, though few if any fibres appear to terminate in the central nucleus. The densest connections would appear to be with PC and PF (cat, Comans and Snow 1981, Graham 1977, McGuinness and Krauthamer 1978, 1980; monkey, Benevento and Fallon 1975, Harting et al 1980). In the cat and

tree shrew the pretectum has been shown to project strongly to CL, and less so to PC (Berman 1977, Itoh 1977, Weber and Harting 1980).

Spinal cord projections to the CIN in placental species are extremely dense, and are apparently entirely or almost entirely restricted to CL (rat, Lund and Webster 1967b; cat, Jones and Burton 1974; prosimian (Galago), Pearson and Haines 1980a; monkey, Boivie 1979). Mehler (1969) compared ascending spinal projections in rat, cat and monkey, and nominated CL as the sole recipient among the CIN of spinal fibres. He considered that earlier studies indicating spinal connections with other parts of the CIN had incorrectly placed the boundaries between CL and adjacent nuclei, and in particular the border between caudal CL and the CM-PF complex. His view is suppported by Jones and Burton (1974) in their study of cat spinal projections. On the other hand,Comans and Snow (1981) have recently demonstrated a very weak spinal projection to PF in the cat, using the retrograde HRP labelling method. The weight of evidence, however, would indicate that the great majority of spinal fibres terminate in CL.

Projections throughout the CIN have been demonstrated from parts of the brainstem reticular formation in the cat (Edwards and de Olmos 1976, Graybiel 1977, Martinez

and Velayos 1981, McGuinness and Krauthamer 1978, 1980). The zona incerta (Ricardo 1981) and parabrachial nucleus, the brainstem centre for taste and/or visceral sensation (Saper and Loewy 1980), have been shown to have widespread connections to the rat CIN.

In the rat a relatively weak projection from the substantia nigra to PF alone among the CIN was seen in the studies of Beckstead et al (1979) and Clavier et al (1976), while in the monkey Carpenter et al (1976) found no evidence for nigral projections to any part of the CIN. In contrast, a number of workers, utilising both retrograde and anterograde tracing techniques in the cat, have demonstrated sparse nigral projections to all CIN subdivisions. These apparently largely overlap the cerebellar projection zones (Comans and Snow 1981, Hendry et al 1979, Lanoir et al 1980, Martinez and Velayos 1981, McGuinness and Krauthamer 1980).

Rather than necessarily accept that these studies indicate interspecies variation, it is also possible to conclude that the differing results may reflect the marked increases in the sensitivity of tracing techniques that have occurred since the earlier rat and monkey studies were conducted. Nigral projections to the CIN would appear to be at best sparse, and thus could easily have escaped detection with the

application of less than maximally sensitive methods.

In the cat CL has been shown to receive connections from a variety of cranial nerve nuclei controlling eye movements, and the trigeminal and vestibular complexes (Berkley 1980, Lanoir et al 1980, Martinez and Velayos 1981). CM and PF also receive trigeminal and vestibular connections, as well as projections from the locus coeruleus (Berkley 1980, Comans and Snow 1981, McGuinness and Krauthamer 1980). Projections from the caudal trigeminal nucleus to CL and CM have been reported in the squirrel monkey (Ganchrow 1978).

The degree of separation of CM and PF into distinct structural entities in different animals is reflected in the distribution of some afferent connections to these centres. In the rat, which has no distinct CM, projections from the entopeduncular nucleus, the presumed nonprimate equivalent of the internal pallidal division, terminate heavily in the lateral part of PF (Carter and Fibiger 1978). In the cat and monkey the entopeduncular nucleus and internal pallidal segment respectively project strongly to CM, with only a minor input to PF (cat, Hendry et al 1979, Larsen and McBride 1979, Nauta 1979; monkey, De Vito and Anderson 1982, Kim et al 1976, Kuo and Carpenter 1973.). The pattern of pallidal projections, then, supports the widely held

belief that CM has been derived, in carnivores and primates, from the lateral part of PF (see Mehler 1966 for discussion). In contrast to the pallidal connections, a major ascending pathway from the periaquaductal grey (PAG) terminates in PF in the cat and monkey, with little or no input to CM (Comans and Snow 1981, Hamilton 1973, Mantyh 1983, McGuinness and Krauthamer 1980).

A tendency in some species towards separation of some connections is also evident within CL. In the rat, the terminal zone of cerebellar fibres in CL would appear to completely overlap the less extensive spinal terminal field (Faull and Carman 1978, Lund and Webster 1967b, Mehler 1969), though whether this reflects functional overlap on individual or small groups of neurons is not known. In the cat and monkey, on the other hand, cerebellar and spinal afferents clearly terminate in different cell groups (Boivie 1979, Hendry et al 1979, Jones and Burton 1974, Kalil 1981).

The central nucleus alone among the CIN receives a major projection from the ventral tegmental area in the rat (Beckstead et al 1979). Finally, no reference could be found in the literature to afferent connections to IAD in any placental species.

Marsupials

Rockel et al (1972), in their anterograde degeneration study of thalamic afferents in Trichosurus, described strong cerebellar and spinal projections to the CIN, with weaker inputs from the superior colliculus. The cerebellar and collicular projections were distributed throughout the group, but concentrated primarily in C, PC and CL. Spinal fibres were shown to terminate primarily in CL and PF, and to a lesser extent PC. The terminal zones of spinal and cerebellar fibres appeared to overlap, though the cerebellar connections were more extensive.

In Didelphis various studies have demonstrated cerebellar, spinal, reticular formation, collicular and pretectal projections to the CIN. In these studies some CIN boundaries are poorly delineated, and there are also inconsistencies in nomenclature. Consequently, detailed analysis of the organisation of inputs from various sources is difficult. Despite these problems, the patterns of cerebellar and collicular projections to the CIN appear to be similarly organised to those in Trichosurus (Benevento and Ebner 1970, Martin 1969, Martin et al 1974, Mehler 1969, Walsh and Ebner 1973). Pretectal projections have similar terminal fields to those from the colliculus (Benevento and Ebner 1970). Projections from the brainstem reticular formation were

reported by Ebner (cited in Walsh and Ebner 1973) to be widely distributed in the CIN, however the precise terminal zones were not identified. No information is available at present on the input connections of IAD in either Didelphis or Trichosurus.

A problem arises in comparing the organisation of spinal projections in Didelphis and Trichosurus. Mehler (1969) states that in Didelphis, as in placental animals (see above), CL alone among the CIN receives spinal inputs. In marsupials the borders between CL and neighbouring parts of the CIN are not distinct. This is particularly the case with respect to caudal CL and PF. If Mehler's stance is taken to be valid for all mammals we may explain Rockel et al's (1972) finding in Trichosurus of extensive and dense spinal connections with PF (and weaker connections with PC), as being due to misplacement of nuclear boundaries, partial merging of nuclei, or perhaps misinterpretation of fibres of passage as terminals. Alternately, Trichosurus may represent a true variation from the organisation described in Didelphis and other species, in having a major spinal input to PF. The generally high level of comparability in overall thalamic afferent connections between Trichosurus and Didelphis, and between these and at least some placental animals, makes this latter possibility seem unlikely, however.

Summary of Subcortical Afferent Connections and Comparison of Placental and Marsupial Organisation

The evidence available to date suggests that collicular, and possibly reticular formation projections to the CIN are basically similar in many mammalian species. Cerebellar connections may vary in some respects, however among placentals the rat appears to be organised along the same lines as marsupials. With the possible questionable exception of Trichosurus, there is a common mammalian organisation in spinal projections to the CIN. In the rat and marsupials it appears that cerebellar and spinal connections overlap extensively in CL, however in the cat and monkey the terminal zones of these inputs are separated.

(ii) EFFERENT CONNECTIONS

It has long been recognised that the principal efferent connections of the CIN are probably those related to the striatum. In the rat HRP injections in striatum have been shown to produce heavy retrograde labelling of all parts of the CIN, but especially PF and CL (Jones and Leavitt 1974, van der Kooy 1979). In the cat and monkey strong CIN-striatal projections are present,

originating primarily in CM, PF and CL (Jones and Leavitt 1974, Kuo et al 1978, Royce 1978, Sato et al 1979). Recently Hazlett and Bagley (1983) have described thalamostriatal connections in a marsupial, with heavy projections from all divisions of the CIN excepting the rhomboid nucleus, but including IAD, in Didelphis.

The existence of cortical projections from the CIN, on the other hand, has only become universally accepted within the last decade (see Jones and Leavitt 1974). In recent years studies utilising increasingly sensitive anterograde and retrograde labelling techniques have repeatedly confirmed that many areas of cortex receive connections from various divisions of the CIN, although as yet we have only incomplete details on the organisation of some of these connections.

Cortical Relationships of Individual CIN Nuclei

Placentals

In the rat, cat and various monkeys CL has been shown to project widely to cortex, including the somatosensory, motor, prefrontal, limbic and posterior parietal areas (rat, Jones and Leavitt 1974, Saporta

and Kruger 1977; cat, Hendry et al 1979, Itoh and Mizuno 1977, Jones and Leavitt 1974, Macchi et al 1977, Niimi et al 1978, 1981a, Robertson and Kaitz 1981, Tangi et al 1978; monkeys, Jacobson et al 1978, Jones and Leavitt 1974, Jones et al 1979, Kasdon and Jacobson 1978, Kievit and Kuypers 1977, Strick 1975). Reciprocal connections from some or all of these areas to CL have been observed in the cat (Jones and Burton 1974, Kaitz and Robertson 1980, Rinvik 1968b) and various monkeys (Jacobson et al 1978, Jones et al 1979).

The position with CL connections, as well as those of other CIN divisions, to visual cortex is less clear. In the rat no evidence has been found for projections from CL, or any other part of CIN, to visual cortex (Jones and Leavitt 1974). In the cat, however, a number of studies have clearly shown that CL, and some other parts of the CIN, project to various visual cortical areas, though there is some disagreement as to the precise sources of input to specific regions (Itoh and Mizuno 1977, Kennedy and Baleydier 1977, Miller and Benevento 1979, Niimi et al 1981b). Evidence of CIN connections with visual cortex has also been presented in the tree shrew, and the prosimians Galago and Microcebus (Carey et al 1979, Cooper et al 1979). It is tempting to postulate that CIN - visual cortex connections may be primarily a characteristic of those

placental species with highly developed visual systems.

It would appear from studies in the hedgehog (Gould et al 1978) and cat (Niimi and Matsuoka 1979) that CIN nuclei probably do not project to auditory cortex.

In the rat, cat and monkey there is some overlap evident in PC and CL connections to parietal cortex, however PC appears to project mostly to dorsomedial and rostral parts of the hemisphere, including limbic cortex (rat and cat) and the rostral frontal lobe (rat, cat and monkey). (rat, Jones and Leavitt 1974, Saporta and Kruger 1977; cat, Niimi et al 1978, 1981a, Spreafico et al 1981; monkey, Jacobson et al 1978, Kievit and Kuypers 1977). Strong descending connections to PC from these latter areas of cortex have been described in the cat (Kaitz and Robertson 1980, Rinvik 1968b). PC has also been shown to project to the insula in the rat (Saper 1982).

Little information is available on the cortical connections of the central and rhomboid nuclei in different species. In the rat a study by Jones and Leavitt (1974) found that the central nucleus is related mostly to the medial surface of the hemisphere, a situation apparently reflected in the cat (Macchi et al 1977, Niimi et al 1978, Robertson and Kaitz

1981). Projections from the rhomboid nucleus of the rat and cat to regions close to the rostral pole of the hemisphere have been described (Jones and Leavitt 1974, Niimi et al 1981a). It should be noted,however, that homology in different species of the region designated "rhomboid nucleus" is questionable. Where it has been recognised as a distinct cytoarchitectural entity, it has been variously placed by different workers in dorsal, or in ventral relationship to the central nucleus (see Ariens Kappérs et al 1936, p 1130 and compare Jones and Leavitt 1974 with Niimi et al 1981a and Le Gros Clark 1929, with Le Gros Clark 1930). It is possible that the principal efferent connections of the central and rhomboid nuclei are directed to the amygdala (Mehler 1980) and ventral striatum (Newman and Winans 1980a).

PF is apparently related to regions close to the rostral pole of the hemisphere in the rat (Jones and Leavitt 1974), however the same may not be true of the cat (Niimi et al 1981a). The cat CM is reciprocally connected to somatosensory and motor cortex, though principally the latter (Hendry et al 1979, Itoh and Mizuno 1977, Jones and Burton 1974, Macchi et al 1977, Rinvik 1968b,c). CM in monkeys projects to motor cortex, and PF to more rostral areas (Jones et al 1979, Kievit and Kuypers 1977, Strick 1975, 1976a). These projections would appear to be reciprocated by the

respective cortical regions (De Vito 1969, Jones et al 1979).

Marsupials

In Trichosurus we found that PC and CL are connected reciprocally to the parietofrontal (sensorimotor) cortex, the caudal part of the prefrontal area, and the posterior parietal area (Haight et al 1983 and see fig 2b). A limited examination of thalamic connections to parietofrontal cortex in Dasyurus demonstrated PC and CL projections to this region (Haight and Neylon 1981b). Our Trichosurus results, from a large number of experiments, did not enable us to distinguish between the projections of CL and PC. Some cortical HRP injections labelled both nuclei, while some others only labelled one. There was no relationship evident between the injection and thalamic label loci. Thus the overall PC projection field would appear to be identical to that of CL. In Donoghue and Ebner's (1981a) Didelphis study, CL, and less frequently PC, were retrogradely labelled following cortical HRP injections in the "post orbital", parietofrontal and posterior parietal areas, again indicating a degree of overlap of their projections. CL connections with cortex were found to be homotypically organised and reciprocal.

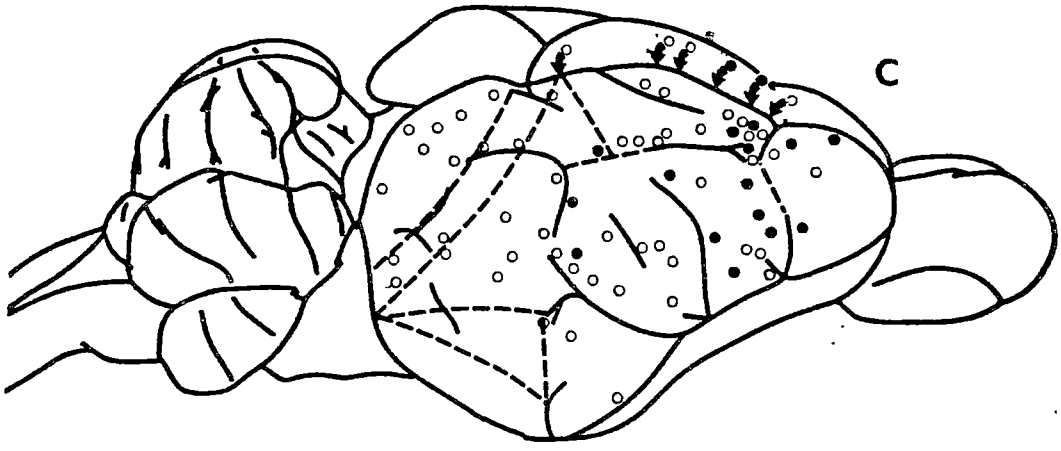
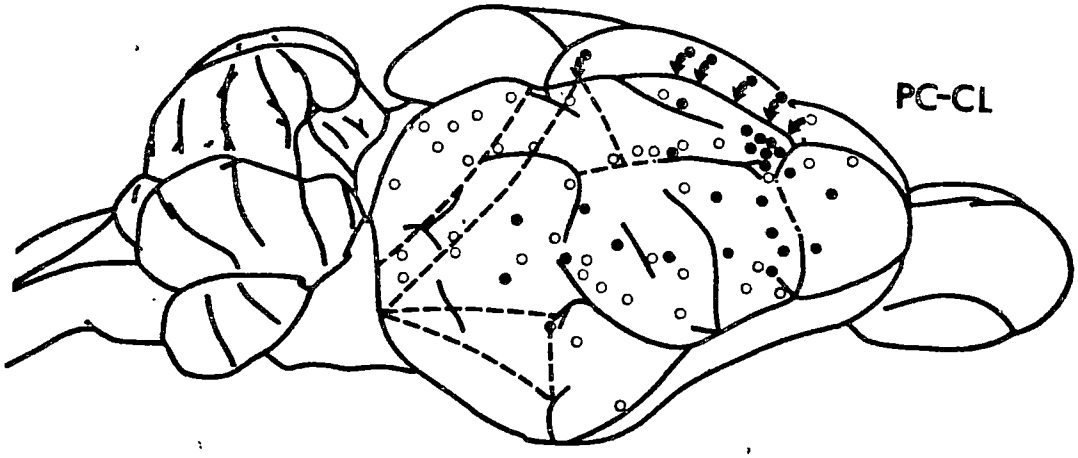


Figure 2

A. Locations of cortical horseradish peroxidase (HRP) injections in Trichosurus resulting in retrograde labelling of the central nucleus indicated by closed circles. Open circles indicate injections producing label in other thalamic centres.



B. Locations of HRP injections resulting in retrograde labelling of the paracentral and centrolateral nucleus (closed circles).

In Trichosurus C is related to the parietofrontal and prefrontal areas, with no apparent preferential distribution (fig 2a). The limited data from Dasyurus suggest that C and RH projections to the parietofrontal area may be primarily directed to its rostral margin. No information is available on the cortical projections of these nuclei in Didelphis.

We found no evidence for PF projections to any of the cortical areas we investigated in either Trichosurus or Dasyurus. Donoghue and Ebner (1981a), however, found in Didelphis that PF projects quite strongly to "post orbital" cortex, immediately rostral to the primary sensorimotor area. No evidence has been found for projections from any part of the CIN to the principal visual areas, or to auditory cortex in marsupials (Aitkin and Gates 1983, Coleman and Clerici 1981, Coleman et al 1977, Haight et al 1980, 1983).

Finally, while IAD in Dasyurus was found to be heavily though discontinuously connected to the parietofrontal area (Haight and Neylon 1981b), no similar projections were seen in our Trichosurus material, nor, as far as is known, have any IAD connections to cortex been described in Didelphis or any placental species. The nucleus does, however, project strongly to the striatum in

Didelphis (Hazlett and Bagley 1983).

Summary of Cortical Relationships and Comparison of Placental and Marsupial Organisation

The distribution of CIN projections to somatic sensory, motor, prefrontal, posterior parietal and limbic cortex appear to be common to the placental animals examined so far. CL is related to all of these regions, however PC, C and RH apparently project preferentially to far rostral and/or medial areas of cortex. In marsupials there is unfortunately no information yet available on CIN projections to rostral parts of the prefrontal area, or to limbic cortex. It is not possible then to delineate the total projection field of individual nuclei in these animals, or to determine which, if any, areas of cortex are preferred targets. The distribution of PC and CL connections to the parietofrontal (sensorimotor) and posterior parietal areas, and to caudal parts of the prefrontal area, is in keeping with the placental organisation, however the presence of significant projections from C and RH to the parietofrontal area in Trichosurus and Dasyurus, but apparently not in Didelphis or placentals, indicates a degree of interspecies variability with respect to the cortical relationships of these nuclei.

There is a problem in comparing PF projections in different animals. In Didelphis this nucleus is related to the "post orbital" area, yet although the equivalent region was examined in Trichosurus, we found no evidence for any PF input. In some, though not all placental animals, PF is apparently primarily related to the rostral extremity of the hemisphere. It is possible that a similar situation may occur in Trichosurus, since if PF projections to cortex exist in this animal, as one might expect to be the case, the elimination of all those cortical areas in which we failed to demonstrate PF inputs leaves few remaining alternatives.

Despite the apparent difference between Didelphis and other animals it is of interest to note that, in none of the marsupials examined, nor in the rat, is PF connected to any significant degree to sensory or motor cortex, while in the cat and monkeys, in which PF and CM are recognisable as separate structures, the latter projects heavily to the motor area.

In certain placental animals, but not marsupials, parts of the CIN are related to visual cortex. It may be a significant point that those placental animals which exhibit such connections have highly developed visual systems. CIN projections to auditory cortex have not

been demonstrated in any species to date.

Finally, there appears to be no parallel in any other species to our finding that IAD projects strongly to the parietofrontal area in Dasyurus.

General Organisation of CIN-Neocortical Projections in Trichosurus and Dasyurus

In our Trichosurus and Dasyurus HRP studies, when label appeared in CIN neurons it was always of relatively high intensity, comparable to that seen in most other thalamic regions.

In neither species did we find evidence for point-to-point projections from any division of the CIN to cortex. Nor did all HRP injections in a given region of cortex label a particular nucleus. On the other hand, widely separated injections often produced label in apparently similar regions within a given nucleus.

The extent of labelling in particular nuclei varied considerably between experiments, and appeared to be unrelated to the cortical injection site, or to the degree of total spread of cortical label. We have previously presented evidence to suggest that the region of effective terminal uptake of HRP following cortical injections is probably limited to a relatively

small zone around the penetration site, and is not related to the apparent total area of spread, provided there is minimal damage to the cortex or underlying white matter (Haight and Neylon 1978b). Similar conclusions have been reported by other authors (Jones and Hartmann 1978 for review).

These findings taken together, point to a number of possibilities :

Firstly, in view of the intensity of labelling, it would seem likely that most individual CIN neurons have fairly restricted terminal zones in cortex, rather than projecting diffusely, or with collateral branches to separate areas. Evidence for such an organisation has also recently been presented for the CIN in the rat and cat (Bentivoglio et al 1981, Steriade and Glenn 1982).

Then, with respect to the apparently inconsistent distribution of CIN connections, some alternate hypotheses present themselves :

In Trichosurus and Dasyurus, and possibly in other Australian marsupials, projections from CIN neurons to the cortex may lack any point to point organisation, but be distributed rather randomly. That neighbouring CIN neurons may in fact project to disparate regions of cortex is indicated by the data from Bentivoglio et al's (1981) double retrograde tracer studies in the cat

and rat. Against this, however, must be placed the evidence for some degree of orderliness, of the cortical connections of CL at least, in the cat (Itoh and Mizuno 1977), and more importantly, in Didelphis (Donoghue and Ebner 1981a).

It could be argued that our findings in Trichosurus and Dasyurus may reflect inaccuracies in the reconstruction and comparison of single cortical injections in a number of animals. However several consistent cortical landmarks are present, particularly in Trichosurus, to allow rather precise reconstruction of injection sites (Haight and Neylon 1978b). In addition, any significant inaccuracy in the relative placements of injections would militate against recognition of orderly projections from other regions of the thalamus. Yet in both Trichosurus and Dasyurus, and particularly the former, where our studies involved comparison of large numbers of experiments, orderly, and in some cases extremely precisely organised projections were observed from a number of thalamic centres, and in particular the ventroposterior complex and dorsal lateral geniculate nucleus (Haight and Neylon 1978b, 1979, 1981b, Haight et al 1980, Neylon and Haight 1983).

An alternate suggestion is that CIN projections may in fact be organised, perhaps highly so, but that certain factors confound analysis of this organisation with the

technique we have used.

Firstly, there is the possibility that significant individual variation may occur in the organisation of connections. If this were the case, recognition of an orderly arrangement would require detailed examination, with multiple tracer techniques, in a single animal, rather than the use of a single tracer in a number of animals, as is the case in our studies. To suggest that such variation may be present is not unreasonable. We have shown that in Trichosurus there may be considerable variability in the nuclear configuration of certain parts of the thalamus, specifically the ventral tier nuclei and their neighbours, and including the CIN, as well as in the degree of gyrencephaly of the cortex (Haight and Neylon 1978c). The regions which show the most obvious variability are those most closely related to somatic sensory and motor functions. That parts at least of the CIN also have an important role in sensory and motor function is evident from the nature of some of their principal inputs. To extrapolate, however, from variability in gross nuclear morphology to significant differences in the ordering of certain thalamic projections to cortex may not be valid. Except in a few cases where severe thalamic distortion was present, we have found considerable consistency between animals in the organisation of

projections from the ventral tier and some other nuclei to regions of cortex which also receive CIN connections (Haight and Neylon 1978b, 1979, Neylon and Haight 1983). If these nuclei retain such consistency in connections, despite morphological variability, why should the CIN be different?

Secondly it may be that CIN projections are extremely specific, with certain neurons or small populations being related to small discrete foci in the cortex that, in some way as yet unknown, are highly specialised, but are scattered within a given cortical area. This could explain the variation seen in the extent and location of CIN labelling, even following apparently closely neighbouring cortical injections. One way of testing this hypothesis would be to place a series of closely spaced injections, each of a separate retrograde label, within a given region of cortex in a single animal.

(iii) FUNCTIONAL CONSIDERATIONS

Our understanding of the overall functions of the CIN requires considerable modification from the earlier concept of the group being a major and rather homogenous component in a widespread and diffuse "non-specific" thalamic projection system to superficial cortical layers, involved in mediating "recruiting responses", and modulating spontaneous cortical

activity (Jasper 1960). It is now evident that individual CIN neurons probably do not project diffusely to cortex, but may have restricted terminal fields (Bentivoglio et al 1981, Steriade and Glenn 1982, present discussion) in deep rather than superficial cortical layers (Herkenham 1980).

CIN nuclei receive inputs from many and varied sources. While some afferent projections to the group are widespread, and possibly overlapping, there is also a tendency, particularly in the cat and primates, towards the direction of certain inputs to individual nuclei or cell groups. Furthermore, individual nuclei may project preferentially, and in at least some cases topographically, to particular regions of cortex (or to subcortical centres, e.g. striatum or amygdala).

Any analyses of CIN function,therefore, must consider that, while in some areas the group may act as a whole, in other respects individual nuclei or perhaps certain groups of nuclei, clearly have separate functional roles. In fact, if the complex were not functionally divisible, one would begin to wonder at the significance of its obvious structural parcellation!

That all CIN nuclei may have some common functions is evidenced by the widespread distribution of projections

from parts of the reticular formation, the parabrachial nucleus, zona incerta and probably substantia nigra, and by the overlap of projections from various nuclei in some regions of cortex.

Most nuclei, however, can be seen to have a unique blend and weighting of connections with other centres, or to be the sole recipients or sources of particular projections, though this may vary somewhat in different species.

Thus, the central (and presumably rhomboid) nuclei are apparently not as closely related to major somatosensory or motor pathways or centres as are other members of the group. The evidence pieced together from studies in a number of species, for heavy afferent projections from the ventral tegmental area (VTA), and for outputs probably directed primarily to medial (limbic) and rostral frontal cortex, and to the amygdala and ventral striatum, would suggest that the principal role for these nuclei is in limbic system functions.

The connections between CL and the spinal cord, spinal trigeminal nucleus, cerebellum, somatic sensory and motor cortex, and striatum clearly show that parts at least of this nucleus are heavily involved in the

somatosensory and motor systems.

The intralaminar region has also been shown to play an important part in visual orientation (head and eye movements) (Hunsperger and Roman 1967, Schlag et al 1974). Projections from pretectum, colliculus and brainstem centres related to head sensation and movements, and other centres controlling eye movements, would indicate that CL and the PF-CM complex, are probably the principal participants in such functions, though perhaps in different ways, as the patterns of afferent and cortical connections differ between the nuclei.

The presence of strong PAG projections to PF, and spinal and caudal trigeminal nucleus connections to CL, as well as the relief of distress due to chronic pain produced by medial thalamic lesions, which in part involve medial elements of the CIN (Sugita et al 1972), would suggest a role for these nuclei in pain transmission, although recent evidence would suggest that the submedius nucleus is probably the medial thalamic region most directly involved with pain (Craig and Burton 1981, Craig et al 1982).

It is not possible, from the information presently available, to make any definite statement about the possible functions of PC. The nucleus shares a number

of afferent and efferent connections with other CIN divisions. The evidence for an apparent preferential distribution of cortical projections to medial (limbic) and rostral prefrontal areas in placental animals indicates some similarities to C and RH. On the other hand, the presence of collicular and cerebellar, though probably not spinal, inputs to PC, and the partial overlap of its cortical projections with those of CL, suggest that comparison is possible between these nuclei. Perhaps PC is some form of functional intermediate between CL, and C and RH, sharing certain aspects of both regions.

The appearance of CM as a distinct nucleus is a characteristic of certain placental species such as the cat and primates, and appears to be closely related to the development of the elaborate motor control systems seen in these animals. CM is clearly an important link between the pallidum (or entopeduncular nucleus) and the striatum and motor cortex. In more generalised mammals such as the rat, PF has similar relationships with the entopeduncular nucleus and striatum, but in this animal, and the marsupials, PF lacks significant connections with motor cortex.

In summary then, on the bases of connections the CIN can now be seen to be implicated in a number of

diverse, though broadly related functions, as integral parts of the circuitry of the somatosensory, motor, limbic, and ocular control systems. In view of the complexity of connection relationships it may be some time before it is possible to assign definitive functions to specific divisions, or to determine how the CIN influences the activities of the cortical and subcortical centres to which the group projects.

(b) MIDLINE NUCLEI

(i) AFFERENT CONNECTIONS

Only limited data are available on afferents to PV in placental animals, from studies in the rat, cat and monkey. These indicate connections from hypothalamus, brainstem reticular formation, parabrachial nucleus and periaqueductal grey (Berk and Finkelstein 1981, Edwards and de Olmos 1976, Hamilton 1973, Mantyh 1983, Saper and Loewy 1980, Saper et al 1979).

Herkenham (1978) showed that the reunient nucleus of the rat has a wealth of inputs from both forebrain and brainstem structures, including those shown above to be related to PV. Most or all of the centres which are sources of PV and RU afferents are considered to subserve "limbic" or "visceral" functions.

At present nothing is known of the input connections of

the midline group in marsupials.

(ii) EFFERENT CONNECTIONS

The efferent connections of the midline nuclei also are primarily directed to "limbic" structures. PV has been shown to be connected to the amygdala in the rat and monkey (Mehler 1980, Ottersen and Ben-Ari 1979), to the ventral striatum (olfactory tubercle and nucleus accumbens) in the rat and hamster (Newman and Winans 1980a, b, Swanson and Cowan 1975), and to the hippocampal formation in the rat and monkey (Amaral and Cowan 1980, De Vito 1980, Segal 1977).

Projections from RU to hippocampus are amply documented in rat and monkey (Amaral and Cowan 1980, Baisden et al 1979, De Vito 1980, Herkenham 1978, Sakanaka et al 1980). RU also projects to medial (limbic) cortex in the rat (Herkenham 1978, Jones and Leavitt 1974) and cat (Niimi et al 1978, Robertson and Kaitz 1981), and to a variety of subcortical forebrain and brainstem centres (Herkenham 1978).

In his retrograde degeneration study of thalamocortical connections in Didelphis Bodian (1942) described a projection from the subparataenial nucleus to rostral

medial cortex. The only other information available at present on marsupial midline group connections is a report of a projection from the intermediodorsal nucleus to the striatum in Didelphis (Hazlett and Bagley 1983).

(iii) FUNCTIONAL CONSIDERATIONS

Information from placental species on the connections of PV and RU show that these nuclei are heavily involved with the limbic system. There is insufficient information to allow comment on possible functions of SPT and the intermediodorsal nucleus, which are not recognised as separate nuclei in many mammals.

MEDIAL NUCLEI

Oswaldo-Cruz and Rocha Miranda (1967) and Bodian (1939), in their descriptions of the *Didelphis* thalamus, placed the parataenial nucleus (PT) with the midline nuclei. Little is known of the connections of this centre, and thus there are few criteria available to justify its placement with any particular group. PT has similar positional relationships to the mediodorsal nucleus (MD), and projects to similar regions of cortex (see below). On these bases, and following the example of Ariens-Kappers et al (1936) in their early review of nervous system structure, and that of Goldby (1941) in his description of the *Trichosurus* thalamus, PT will be included here with MD in the medial group. This treatment should not be taken as necessarily implying any functional relationship between the two nuclei.

1. DESCRIPTIONS AND COMPARISONS OF NUCLEAR STRUCTURE IN MARSUPIALS

(For illustrations see Haight and Neylon 1978a figs 2-7, Haight and Neylon 1981a figs 2-8, Oswaldo-Cruz and Rocha-Miranda figs 3-10).

PT is the first of the medial nuclei to appear in the rostral pole of the marsupial thalamus. It is very

similar in the three marsupials and contains two clear divisions, a lateral cell group containing large cells, and a more compact medial group containing smaller cells. As the anterior nuclei appear PT gives way to MD, which continues caudad to the level of the habenulointerpeduncular tract. Throughout most of its extent MD is surrounded by the midline nuclei medially, the intralaminar nuclei ventrally and laterally, and the habenular nuclei and medullary stria dorsally.

In the caudal thalamus the central and paraventricular nuclei separate in both Dasyurus and in Trichosurus, allowing the two mediodorsal nuclei to touch, but not merge, on the midline. In Didelphis an intermediodorsal nucleus is found on the midline, interposed between the rhomboid, and more caudally the central nucleus and the paraventricular nucleus. Otherwise, MD is similar in the three animals.

The cytoarchitecture of MD is very irregular. Cells are isolated into subgroups by the large number of fibre bundles criss-crossing the nucleus. This gives the impression of many subdivisions. However, as we have noted in Trichosurus (Haight and Neylon 1978a), these are not reproducible from animal to animal, or even from right to left within the same animal.

2. CONNECTIONS AND FUNCTIONS OF THE MEDIAL NUCLEI

(a) MEDIODORSAL NUCLEUS

(i) SUBCORTICAL AFFERENT CONNECTIONS

Placentals

In the rat (Krettek and Price 1977a), cat (Niimi and Kuwahara 1973, Niimi et al 1981a) and primates (Simmons 1980 for recent review and see other references below), MD contains consistent cytoarchitectural divisions with specific connection patterns. Interspecies comparison of these divisions is difficult,however, as they vary in number, position, and in their relationships to particular afferent and efferent connections in each case. MD has also been subdivided on the basis of connection patterns in the guinea pig (Markowitsch and Pritzel 1981) and rabbit (Benjamin et al 1978, Jackson and Benjamin 1974), however no parallel cellular parcellation is evident in these animals.

In the rat, rabbit, cat and some monkeys, it is clear that MD can be broadly divided into medial and lateral functional zones on the basis of afferent connections. The medial zone alone has been shown to receive major projections from olfactory centres (rat, Heimer 1972, Krettek and Price 1974, 1977b, Leonard 1972; rabbit, Jackson and Benjamin 1974; cat, Guillery 1959; monkeys, Benjamin and Jackson 1974), the amygdala (rat,

Krettek and Price 1974, 1977b; monkey, Porrino et al 1981), and the ventral tegmental area (VTA) (rat, Beckstead et al 1979; cat, Velayos and Reinoso-Suarez 1982). Direct projections from the amygdala and ventral tegmental area (VTA) to cortex overlap those from MD in the rat and cat (Divac et al 1978b, Krettek and Price 1974, 1977b), and the monkey. In the monkey these projections overlap only those from the medial part of MD (Porrino et al 1981). In the rat and monkey the amygdala and VTA projections appear not to extend beyond the MD field, although this is not the case in the cat (Markowitsch and Irle 1981). It would seem then that the medial region of MD is an integral part of a system of direct and indirect connections between important limbic structures and cortex.

More lateral parts of MD, on the other hand, receive somewhat different projections and are related to separate regions of cortex (see below). Development of the lateral parts of MD is most pronounced in the cat and primates, and particularly the latter (Niimi and Kuwahara 1973, Simmons 1980).

Apart from the olfactory, amygdalar, and VTA projections mentioned above (and see also Arikuni and Gotow 1979 (rabbit); Fallon and Ribak 1980, Goldschmidt and Heimer 1980, Siegal et al 1977 (rat); Sapawi and

Divac 1978 (tree shrew)) MD receives a number of other inputs.

Projections to unspecified parts of the nucleus from the hypothalamus and thalamic reticular nucleus have been shown to be present in the rabbit (Arikuni and Gotow 1979) and tree shrew (Sapawi and Divac 1978). Also in the tree shrew MD receives projections from the central grey, raphe nuclei, and locus coeruleus (Sapawi and Divac 1978). In the cat connections from these, and other parts of the brainstem tegmentum, have been shown to be related to either intermediate or lateral, or both, regions of MD (Velayos and Reinoso-Suarez 1982). The interpeduncular nucleus has been shown to project heavily throughout MD in the cat (Velayos and Reinoso-Suarez 1982), as has the deep mesencephalic nucleus in the rat (Veazey and Severin 1980).

Extensive inputs from the substantia nigra to MD were demonstrated by Velayos and Reinoso-Suarez (1982) in the cat, using the retrograde tracer method, however the anterograde labelling study of Hendry et al (1979) did not show any nigral projections to MD. In the rat nigral projections to paralaminar (adjacent to the internal medullary lamina) parts of the nucleus were demonstrated by Beckstead et al (1979), though not by Clavier et al (1976). Carpenter et al (1976) reported a significant nigral projection to paralaminar MD in

the monkey.

Other centres which could be specifically related to the paralaminar region of MD include the cerebellum (rat, Faull and Carman 1978), spinal cord (rat, Lund and Webster 1967b; cat, Jones and Burton 1974; prosimian (Galago), Pearson and Haines 1980a), and caudal trigeminal nucleus (monkey, Ganchrow 1978). Projections to paralaminar MD have also been described from deep layers of the superior colliculus, and some other brainstem centres thought to be related to control of eye movements (cat, Graybiel 1977, Velayos and Reinoso-Suarez 1982; monkey, Harting et al 1980). These latter connections are significant in light of the relationship between paralaminar MD and the frontal eye fields of the cortex (Divac et al 1978b, Kunzle and Akert 1977, Markowitsch et al 1980b, Scollo-Lavizzari and Akert 1963). A note of caution is necessary, however, with respect to some projections to paralaminar MD. Studies, other than those mentioned above, of the thalamic connections of the cerebellum, spinal cord and superior colliculus, have demonstrated projections to the intralaminar nuclei, but not to adjacent parts of MD (cat, Graham 1977, Hendry et al 1979; monkey, Boivie 1979, Kalil 1981). This confict may arise, in part at least, from difficulties and differences in the determination of nuclear boundaries.

Marsupials

No anatomical data could be found in the literature on subcortical afferent projections to MD in marsupials. Jackson et al (1978) have provided physiological evidence for an extensive olfactory system input to the nucleus in Didelphis.

(ii) CORTICAL RELATIONSHIPS

Placentals

MD projects to the prefrontal cortex. In fact it was the lack of definitive cytoarchitectural characteristics in rostral parts of the neocortical mantle in non primates that led Rose and Woolsey (1948) to suggest that the prefrontal ("orbitofrontal") region should be defined as that area of cortex which receives MD connections. This definition, based on connective rather than structural criteria, appears to have received wide acceptance, although some workers have recently questioned whether it is totally appropriate, largely because much of the MD projection field is now known to also receive substantial connections from other thalamic centres, including the anteromedial nucleus (Divac et al 1978b, Guldin et al 1981, Krettek and Price 1977a).

The total MD projection field in all the placental species examined so far is essentially similar, extending over the medial and ventromedial, lateral and ventrolateral, polar and in some cases dorsal surface of the hemisphere immediately rostral to, and in some cases at least, apparently slightly overlapping the motor areas. In non primates the field can be envisaged as a U shaped area of cortex oriented horizontally, with the base of the U at the rostral pole. In the cat, and perhaps the rat, the area may be divided into two separate strips of cortex. In primates and in the tree shrew, the field is expanded to include more dorsal parts of cortex (tree shrew, Divac and Passingham 1980, Divac et al 1978a; mouse, Guldin et al 1981; guinea pig, Markowitsch and Pritzel 1981; rat, Divac et al 1978b, Krettek and Price 1977a; rabbit, Arikuni and Ban 1978, Benjamin et al 1978; cat, Markowitsch et al 1978, 1980a, Martinez-Moreno and Reinoso-Suarez 1977, Niimi et al 1981a; prosimian (Galago), Markowitsch et al 1980b; monkey, Kievit and Kuypers 1975, 1977, Tobias 1975).

MD receives descending connections from those areas of cortex to which it projects (rat, Siegel et al 1977; rabbit, Arikuni and Gotow 1979; tree shrew, Sapawi and Divac 1978; primates, Jacobson et al 1978, Leichnetz and Astruc 1975).

In several placental species MD's cortical projections have been shown to have an orderly arrangement. Details of the organisation may vary somewhat in different animals, however there are also some basic similarities. For example, in the guinea pig medial MD projects to lateral prefrontal cortex, in the vicinity of the rhinal sulcus (fissure), while lateral MD is related to the medial wall and the rostral pole of the hemisphere (Markowitsch and Pritzel 1981). In the rabbit and rat medial parts of MD again project to the lateral sulcal area, but also to a restricted area in the rostral ventral part of the medial surface. Lateral MD is related to more caudal and dorsal parts of the medial surface (rabbit, Benjamin et al 1978; rat, Beckstead 1976, Divac et al 1978b, Krettek and Price 1977a).

In the prosimian Galago, projections from medial, lateral and paralaminar parts of MD in turn appear to terminate in a series of horizontally oriented strips of cortex passing from medial to lateral surfaces around the rostral pole, and arranged in sequence from ventral to dorsal. In this species, lateral parts of MD project to both medial and lateral parts of the prefrontal area (Markowitsch et al 1980b). A similar organisation to Galago is seen in the rhesus

monkey, although in this case the prefrontal area is considerably larger, and the projection strips are arranged more vertically, with a progression of projections from medial, lateral, and paralaminar MD, correspondng to a rostral to caudal sequence of transverse strips of cortex (Kievit and Kuypers 1975, 1977, Tobias 1975).

In the cat, examination of the data from the HRP studies of Markowitsch et al (1978), Martinez-Moreno and Reinoso-Suarez (1977) and Niimi et al (1981a), does not immediately suggest close similarities to other species in the pattern of MD-cortical connections. In combination however, their data provide a picture of an organisation somewhat similar to that seen in Galago. A fundamental difference between the cat and other species is found in the presence of a discontinuous MD field on the lateral surface of the hemisphere (Markowitsch et al 1980a).

Marsupials

In Trichosurus, anterograde and retrograde degeneration studies have shown that MD projects to both medial and lateral surfaces of the rostral pole of the hemisphere, in front of the sensorimotor area (Broomhead 1974, Goldby 1943). Our HRP material confirms an MD projection to the lateral cortex. We have insufficient

data to comment on possible projections to the medial wall of the hemisphere. The MD projection field as shown in our Trichosurus material encroaches slightly onto the rostral margin of the parietofrontal (sensorimotor) area (Haight et al 1983 and see fig 3).

In Dasyurus we have not examined projections to areas rostral to the parietofrontal cortex, however one HRP injection into the border zone between this area and prefrontal cortex produced heavy labelling in MD, as well as in VL (Haight and Neylon 1981b).

In Didelphis both retrograde degeneration and HRP studies have shown that MD projects heavily to a rostral lateral area of cortex (Bodian 1942, Divac et al 1978a, Pubols 1968). These studies did not investigate the medial surface of the hemisphere. The anterograde degeneration study of Tobias and Ebner (1973) supports the findings of the other workers and indicates that MD projections are in fact limited to lateral areas of cortex. The significance of this finding will be discussed at a later point. Donoghue and Ebner (1981a) found that there is overlap of projections from MD and ventral tier nuclei in the 'post orbital' area in Didelphis.

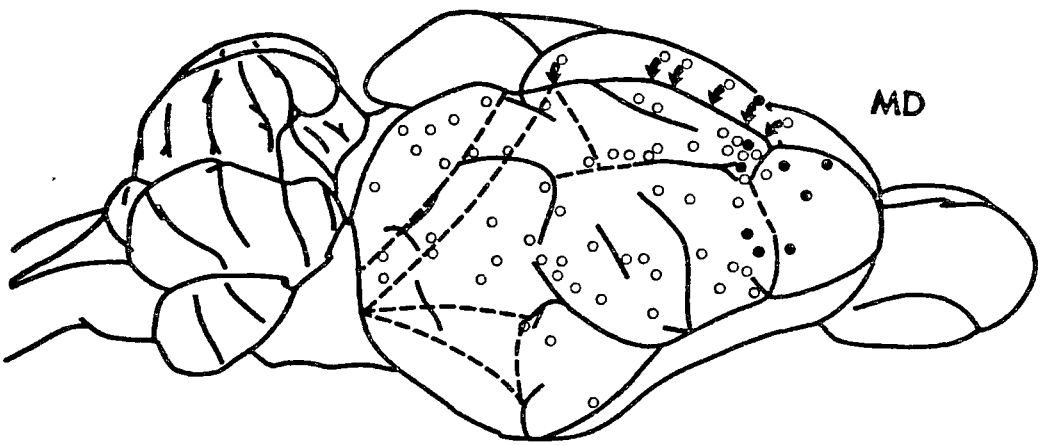


Figure 3

Cortical HRP injections in Trichosurus which produced retrograde labelling in the mediodorsal nucleus (closed circles).

Summary of Cortical Relationships and Comparison of Placental and Marsupial Organisation

If one accepts Rose and Woolsey's (1948) definition of prefrontal cortex, as being that area which receives MD projections, then the prefrontal area is similarly located, though variable in extent, in all the placental species examined to date, and in Trichosurus. In these animals the MD field extends over the medial, rostral and lateral surfaces of the hemisphere. The lateral part of Trichosurus prefrontal area would appear to include a relatively large area of cortex compared to most non primates. Didelphis differs from the other species examined to date in having a prefrontal area apparently restricted to the lateral surface of the hemisphere.

In marsupials, and in a number of placental animals, it would appear that MD projections may slightly overlap the rostral margin of the sensorimotor area.

The information available from studies in marsupials does not allow any definite statements on the possibility of homotypical relationships between MD and cortex. Such relationships are evident in many placentals, although their organisation varies somewhat between species.

At this point it is appropriate to comment on the apparently restricted extent of the prefrontal area in Didelphis. As previously stated, in a number of placental animals medial parts of MD receive major olfactory and limbic projections. Jackson et al (1978) have provided evidence that in Didelphis olfactory projections are distributed throughout MD, indicating that, if this animal follows what is apparently a common mammalian plan, the equivalent of the medial "olfactory-limbic" functional zone of other species probably occupies most or all of the nucleus. The finding of Tobias and Ebner (1973) that the MD projection field or prefrontal area in Didelphis is restricted to the lateral surface of the hemisphere is therefore not surprising, since in the guinea pig, rabbit and rat, medial ("olfactory-limbic") MD is related solely or principally, to lateral areas of cortex.

One could speculate,then,that Didelphis may represent an extremely primitive level of development of the MD prefrontal cortex system, since an increase in the relative size of lateral parts of MD, and of the areas of cortex they project to, would appear to be characteristic of more advanced forms. The presence of a significant MD projection to medial cortex in Trichosurus could be taken as indicating a considerable

advance in development from Didelphis, especially if it could be shown that this projection originates primarily from lateral parts of the nucleus. We have no direct evidence to suggest that this may be the case, however in our HRP material, injections into the lateral surface of the hemisphere never labelled the far lateral margin of MD. Instead,label fields were always confined to the ventromedial part of the nucleus. This leaves open the question of where the lateral margin of MD projects. Goldby's (1943) retrograde degeneration study indicates that this region is related to the rostral pole of the hemisphere, however this does not exclude the possibility of additional projections to the medial surface.

Clearly, our understanding of the evolution of MD and the prefrontal area in mammals could be greatly enhanced by a careful examination of both the input and output relationships of MD in marsupials and the more generalised placental animals.

(iii) FUNCTIONAL CONSIDERATIONS

Attempts have been made to analyse some functions of the prefrontal area, using selective ablation and stimulation techniques in animals (e.g. Passingham 1978, Wikmark et al 1973). Some parts of this area,

and hence some at least of its connections, possibly including those with MD, are evidently involved in memory processes (see Eccles 1978, Jacobsen et al 1978 for discussions). There is some more direct evidence for MD involvement in memory circuitry from diencephalic lesion studies, although this is by no means conclusive (Squire 1982 for recent review). The results of leucotomy in humans have been amply documented (e.g. Robinson and MacDonald 1975). This procedure has been mainly performed on patients suffering from severe psychiatric disturbances, who therefore can hardly be considered as 'normal' subjects. The effects are nevertheless similar to those produced by disease or trauma to the frontal lobes. Post operatively, leucotomy patients tend to display reduced intellectual abilities of various kinds, impairment of recent memory, and emotional changes. These results implicate the prefrontal cortex, and by inference the MD-prefrontal system, in a number of extremely complex aspects of behaviour. A number of factors confound more detailed functional analysis of the MD-prefrontal system. These include: the difficulties inherent in analysing the complex behavioural deficits resulting from manipulation of the circuitry; our present poor level of understanding of the organisation of the circuitry in question; the interspecies variability apparent in the precise

location and extent of the prefrontal area, and of the projection fields of different centres connected to it; and the presence of subdivisions in both MD and cortex, each apparently having distinct functional roles (Larsen and Divac 1978).

Leucotomy has also had a limited application in cases of severe chronic pain (e.g. Freeman and Watts 1946). In these cases the level of distress is reduced, although awareness of the pain remains. Medial thalamotomy, involving lesions which in part encroach on MD, as well as elements of the central intralaminar nuclei, have been found to afford relief from chronic pain (Sugita et al 1972). In addition,Lewis et al (1983) have recently reported a close correspondence between the laminar distribution of opiate receptors and MD terminals in the prefrontal cortex of the rat. This would suggest some role for the nucleus in opiate mediated pathways, perhaps including those related to pain transmission. Counter to this, however, is evidence that the submedius nucleus may be the medial thalamic centre most directly involved in pain circuitry (Craig and Burton 1981, Craig et al 1982).

Parts at least of MD and prefrontal cortex are involved in major ascending pathways from the brainstem, as evidenced by the strong ventral tegmental area projections to these regions, and the presence in the

prefrontal area of high levels of catecholamines, presumably located in axons of brainstem origin (Berger et al 1976, Divac et al 1978a).

The functional significance of these pathways unfortunately remains obscure, although they may be involved in "motivational" and "emotional" processes (see Markowitsch and Irle 1981 for recent discussion). Connections to MD from the locus coeruleus (LC) indicate some role in the ascending noradrenergic projection system, however MD is by no means unique in this regard. LC projections appear to be extremely widespread, connecting to several other thalamic centres and most areas of cortex. As yet no definitive function has been assigned to these LC projections (Markowitsch and Irle 1981).

(b) PARATAENIAL NUCLEUS

CONNECTIONS AND FUNCTIONS

Nothing is known of the afferent or efferent projections of PT in marsupials. The situation with respect to afferent connections in placentals is only marginally better. A search of the literature has to date only unearthed mention of a pathway from the lateral hypothalamic area to PT in the rat (Saper et al

1979).

Information on the outputs of PT has been somewhat easier to find, but the available data contain numerous inconsistencies.

It is clear that PT projects strongly to anteromedial, and possibly polar regions of the prefrontal cortex in rodents and in the rabbit. The projection field is totally contained within that of MD in these animals (mouse, Guldrin et al 1981; guinea pig, Markowitsch and Pritzel 1981; rat, Beckstead 1976, Divac et al 1978b, Jones and Leavitt 1974; rabbit, Benjamin et al 1978). In the cat, on the other hand, PT appears to project only weakly to cortex, being related to both lateral and medial parts of the prefrontal area (Niimi et al 1981a). A connection from PT to the hippocampus has been described in the monkey (Amaral and Cowan 1980), however in the rat two HRP studies have given no indication of such a pathway (Baisden et al 1979, Segal 1977), and in a third study, Sakanaka et al (1980) state that PT neurons were retrogradely labelled only by HRP injections which spread beyond the hippocampus into adjacent cortex or thalamus.

Similarly, PT projections to the amygdala appear to be present in the rat and cat (Ottersen and Ben-Ari 1979),

but not the monkey (Mehler 1980). Finally, PT connections to the ventral striatum (olfactory tubercle and nucleus accumbens) have been reported in the hamster and rat (Newman and Winans 1980a,b, Swanson and Cowan 1975). Whether these pathways are present in all other species or also subject to variation remains to be seen.

The connections that have been demonstrated to date show that PT probably plays some part in limbic system circuitry. Careful comparative studies of input and output relationships are needed to determine whether the connections, and hence presumably the functions, of the nucleus really are subject to the degree of variability indicated by the presently available information.

ANTERIOR NUCLEI

This group includes the anterodorsal (AD), anteroventral (AV) and anteromedial (AM) nuclei. As noted previously, the interanterodorsal nucleus has been removed from this group and placed with the central intralaminar complex.

1. DESCRIPTION AND COMPARISONS OF NUCLEAR STRUCTURE IN MARSUPIALS

(For illustrations see Haight and Neylon 1978a figs 2-4, Haight and Neylon 1981a figs 2-4, Oswaldo-Cruz and Rocha-Miranda 1967 figs 4-6).

With the exception of AM, the nuclei of the anterior group are very similar in Didelphis, Dasyurus and Trichosurus.

AD is easily identified as a small but very distinct group of densely packed and darkly stained cells related to the internal medullary lamina (iml) on the dorsal surface of the rostral thalamus. The much larger AM and AV occupy the rostral pole of the thalamus and lie lateral and ventral to the iml. They are replaced caudally by the ventroanterior and laterointermediate nuclei. In the two polyprotodont species there is no distinct boundary between AM and

AV, which have similar cytoarchitecture, however in Trichosurus fibres of the mamillothalamic tract clearly separate the two nuclei from each other, and from the ventroanterior nucleus.

In Trichosurus AM has a prominent caudal extension, which is not evident in the other two animals. For purposes of comparison, the thalami of a number of other Australian marsupials were examined. The Trichosurus type of AM configuration was found also to be present in some other advanced diprotodont species (wallaby, Macropus eugenii; ringtailed possum, Psuedochirus peregrinus and wombat, Vombatus ursinus), but not in any of the available polyprotodonts (marsupial mice Antechinus swainsonii and Sminthopsis leucopus; Tasmanian devil, Sarcophilus harissii; bandicoots Perameles gunii, Isoodon obesulus). Goldby (1941), in his description of the Trichosurus thalamus, recognised the region in question as part of AM, but later (Goldby 1943) renamed it "nucleus ventralis pars medialis" (ventromedial nucleus), to correspond to the cell group given this name by Bodian (1939) in Didelphis. On the basis of its common cortical projections and cytoarchitectural continuity with the remainder of the nucleus, we have reinstated the region as part of AM (Haight and Neylon 1978a, Haight et al 1983). As will be discussed later (see Ventral Nuclei)

Bodian's (Didelphis) ventromedial nucleus, and equivalent regions in Dasyurus and some other Australian marsupials, are distinct from both AM and the ventromedial nucleus, and probably correspond to the submedius nucleus of various placental species.

Lying between AM and the subparataenial nucleus in Didelphis is a small but obvious region comprising sparse, lightly stained cells. Oswaldo-Cruz and Rocha-Miranda (1967) have termed this area Nucleus B. Knowing that such a region has been identified in Didelphis enables one to locate a similar, but much less distinct, region in Dasyurus. Its presence in Trichosurus is doubtful.

2. CONNECTIONS AND FUNCTIONS OF THE ANTERIOR NUCLEI

(i) SUBCORTICAL AFFERENT CONNECTIONS

Placentals

That the anterior group receives massive projections from the mamillary bodies in placental animals has long been known. It is now apparent that these projections are highly organised, with different regions of the mamillary complex being related to specific nuclei or

regions of nuclei (Cruce 1975, Watanabe and Kawana 1980). In addition, it appears that the hippocampal formation supplies direct connections to the anterior group, primarily to AV, as well as the more familiar pathways to the mamillary bodies (Irle and Markowitsch 1982, Siegal and Tassoni 1971, Swanson and Cowan 1977).

Irle and Markowitsch (1982) have recently examined the afferent connections of the anterior nuclei in the cat using the retrograde HRP method. Unfortunately their study does not differentiate between the individual nuclei of the group, and also suffers from possible label contamination of the mediodorsal nucleus, and presumably some parts of the intervening intralaminar region. Retrograde labelling of neurons in the amygdala and septal area following their injections into the anterior group confirms other reports of connections from these centres, apparently primarily to AM (Porrino et al 1981, Powell 1973). Label also appeared in a number of other thalamic nuclei. Some of these centres, the midline and central nuclei, had been shown previously to project to AD in the cat (Hajdu and Hassler 1973).

Irle and Markowitsch (1982) also reported that their injections produced moderate to heavy labelling of the ventral tegmental area, thalamic reticular nucleus, periaqueductal grey, substantia nigra, locus coeruleus

and deeper layers of the superior colliculus, with lighter labelling of the interpeduncular nucleus, raphe nuclei, parabrachial nucleus, and anterior hypothalamus. Such findings are of doubtful significance, since these centres project to either or both of the mediodorsal nucleus, and the intralaminar region (see Central Intralaminar and Medial Nuclei), which may have also been labelled in their study. Also, anterograde tracer studies of projections from the ventral tegmental area in the rat (Beckstead et al 1979), and the substantia nigra (Hendry et al 1979) and superior colliculus (Graham 1977) in the cat, do not indicate projections from these centres to the anterior nuclei, however such negative findings may simply reflect differences in sensitivity between the anterograde and retrograde tracer techniques.

Marsupials

No information could be found in the literature relating to afferent connections of the anterior nuclei in marsupials, however it would seem likely that the major inputs are similar in all mammals. Certainly the mamillothalamic tract is a prominent feature of the thalamus in the marsupial species examined so far.

(ii) CORTICAL RELATIONSHIPS

Placentals

The cortical projections of the anterior nuclei are essentially similar in all the placental mammals examined so far. The terminology applied to the dorsomedial region of the cortex which receives anterior group connections may vary slightly between studies or animals, however the total projection field encompasses what are referred to by most authors as the anterior limbic, cingulate, and retrosplenial areas. These form a strip of cortex related rostrally, dorsally, and caudally to the corpus callosum in the medial wall of the hemisphere. AM projects primarily to rostral parts of this strip, partly overlapping the caudal extent of the MD field. AV and AD project mainly to more caudal areas. The terminal fields of the three nuclei overlap to some extent (mouse, Guldin et al 1981; guinea pig, Markowitsch and Pritzel 1981; rat, Beckstead 1976, Divac et al 1978b, Domesick 1972, Krettek and Price 1977a; rabbit, Benjamin et al 1978, cat, Niimi 1978, Niimi et al 1978, Robertson and Kaitz 1981; monkey, Yakovlev et al 1960, 1966). Descending projections to the anterior group from these areas of cortex are generally, though probably not exactly, reciprocal (rat, Domesick 1972; cat, Irle and Markowitsch 1982, Kaitz and Robertson 1980; monkey,

Powell 1973).

Kasdon and Jacobson (1978) have described a projection from the anterior group to the inferior parietal lobule in the monkey. No other reference to similar connections in this or other species could be found in the literature.

The anterior nuclei project strongly to the hippocampal formation, probably primarily to the subicular region. Some authors feel that these connections may be more substantial than those to dorsomedial areas of cortex (guinea pig, Shipley and Sorensen 1975; rat, Domesick 1972, Sakanaka et al 1980; cat, Irle and Markowitsch 1982; monkeys, Amaral and Cowan 1980, De Vito 1980).

Marsupials

Bodian (1942), in his retrograde degeneration study of thalamic projections in Didelphis, concluded that the anterior nuclei project to the "interhemispheric" region (medial surface of the hemisphere), with AM projecting to rostral, and AD and AV to more caudal areas of cortex. Didelphis then apparently follows the placental organisation pattern.

The data from Goldby's (1943) retrograde degeneration

study in Trichosurus are less conclusive, although he felt that the pattern of anterior group projections was probably similar to that of other mammals. Of particular interest however is that some of his experiments (see in particular nos. P11 and P47) indicate a degree of overlap of AM projections onto the medial parietofrontal and dorsal (lateral) prefrontal areas. In our Trichosurus HRP material injections into these regions of neocortex heavily labelled AM neurons (Haight et al 1983 and see fig 4). Overlap of AM projections onto the parietofrontal area is even more obvious in Dasyurus where HRP injections in the rostromedial margin of this area, on the lateral surface of the hemisphere, produced heavy labelling in AM (Haight and Neylon 1981b). In both Trichosurus and Dasyurus the AM projection field clearly partly overlaps that of MD. The apparent restriction of MD projections to the lateral surface of the hemisphere in Didelphis (see Medial Nuclei) means that such overlap may not be present in this animal.

Goldby (1943) found no evidence for any cortical connections from the caudal extension of AM in Trichosurus, a result which led him to redesignate this cell group as the "nucleus ventralis pars medialis", as discussed previously. In our Trichosurus HRP material however, this region was consistently labelled, together with more rostral parts of the nucleus (Haight

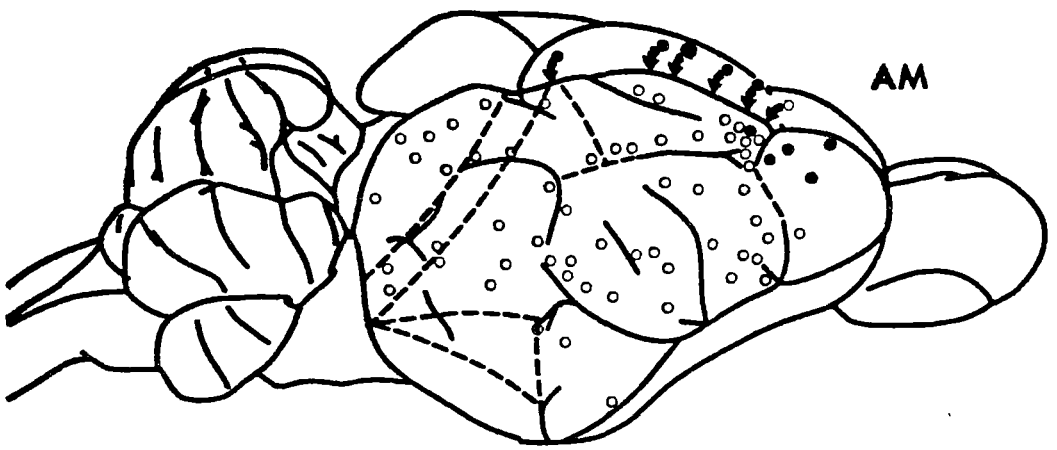


Figure 4

Cortical HRP injection in Trichosurus which resulted in retrograde labelling of the anteromedial nucleus (closed circles).

et al 1983).

Finally, no information is available concerning possible anterior group projections to the hippocampus in marsupials.

Summary of Cortical Relationships and Comparison of Placental and Marsupial Organisation

The distribution of projections from the anterior nuclei to parts of the deep medial wall of the hemisphere is similar in the placental species examined to date. Among the marsupials Didelphis at least would appear to conform to the placental organisation. The presence of AM projections the parietofrontal area in Trichosurus and Dasyurus, and onto the dorsal (lateral) surface of the prefrontal area in Trichosurus, however, represents an important departure in these species from the general mammalian organisation. With the exception of one report of anterior group connections to the inferior parietal lobule of the monkey (Kasdon and Jacobson 1978), all available evidence indicates that the AM field in other species is limited to the deep medial wall of the hemisphere and hippocampal formation.

Trichosurus and Dasyurus do show a similarity to

placentals in that the AM and MD projection fields overlap to some extent. It seems likely that this is not true of Didelphis, due to the apparent restriction of the AM and MD projection fields to the medial and lateral walls of the hemisphere respectively.

(iii) FUNCTIONAL CONSIDERATIONS

Few students of neuroanatomy would be unfamiliar with Papez' (1937) classical concept of a major limbic circuit related to "emotion", comprising a loop of connections between hippocampus, mamillary bodies, anterior thalamic nuclei and cingulate cortex. The "Papez loop" has for many years provided some basis for understanding the functions of its constituent elements, including the anterior nuclei. In recent times, however, its value as a model has been greatly diminished, as the principal elements of the proposed circuit are now known to have have substantial connections with other centres, and to be interconnected in a far more complex way than was originally conceived (Irle and Markowitsch 1982). The anterior nuclei and their connections are probably involved in many functions, perhaps including those originally attributed to them by Papez. In particular they appear to be important elements in circuitry related to memory functions (see Eccles 1978, Irle and

Markowitsch 1982).

VENTRAL NUCLEI

This group comprises the ventroanterior (VA), ventrolateral (VL), ventroposterior (VP) and ventromedial (VM) nuclei. For convenience the submedius nucleus (SM) is also treated in this section. Since the only known afferent connections to SM derive from somatosensory pathways, this procedure seems reasonable.

1. DESCRIPTIONS AND COMPARISONS OF NUCLEAR STRUCTURE IN MARSUPIALS

(For illustrations see Haight and Neylon 1978 figs 4-10, Haight and Neylon 1981a figs 4-11, Oswaldo-Cruz and Rocha-Miranda 1967 figs 6-13).

VA is the first of the ventral tier nuclei to appear in the rostral part of the thalamus, lying at the ventrolateral margin of the anteroventral (AV) and anteromedial (AM) nuclei. At more caudal levels the rostral pole of VL displaces VA dorsomedially, to replace AV and AM. VA is then in turn replaced by the main body of VL. In both Trichosurus and Dasyurus VA is easily distinguished from adjacent nuclei by the close packing of its cells. In Didelphis VA is identified only with difficulty, however careful

comparison of our Didelphis material with that from the other two species shows that the nucleus is similar in shape and location in each case.

VL in the three species is characterised by scattered groups of cells interspersed between the numerous fibre bundles traversing the nucleus. In Trichosurus a distinct cell dense region is present in the anteromedial part of VL (Haight and Neylon 1979). This 'internal' division (VLi) is not evident in the other species.

The difficulty in differentiating between VA and VL in Didelphis has led to varying treatment of these regions in different studies. Oswaldo-Cruz and Rocha-Miranda (1967) recognised both nuclei, but considered them to be distinguishable as separate entities only at the rostral and caudal extremes respectively of the complex they designated 'nuclei ventralis lateralis' (xVL). With few exceptions (e.g. Coleman et al 1977) other workers have not considered the nuclei separately, and have applied various terms to the complex thus formed; 'nucleus ventralis anterior' (Bodian 1939, Pubols 1968), 'ventral anterolateral nucleus' or 'VAL' (Killackey and Ebner 1973, Walsh and Ebner 1973) and 'nucleus ventralis lateralis' or 'ventral lateral complex' (Diamond and Utley 1963, Donoghue and Ebner 1981a, b). This treatment of VA and VL as a single

structure creates some difficulties in comparing the connections of these regions with those in other species.

Oswaldo-Cruz and Rocha-Miranda (1967) considered that their xVL in Didelphis extended some distance over the dorsolateral margin of VP. Careful examination of our Didelphis material does not support this conclusion. The caudal boundary of VL, while not being as easily distinguished as that in the two Australian species, is nevertheless clearly recognisable and similarly placed. Their caudal extension of xVL would appear to correspond in part to the posterior nucleus (PO) of Trichosurus and Dasyurus, and to equivalent regions in other species (Haight and Neylon 1978a, 1981a, Neylon and Haight 1983).

The transition from VL to VP is quite distinct and abrupt, particularly in the two Australian species, being marked by the replacement of the scattered cell groups and fibre bundles of the former nucleus with the relatively closely packed and uniformly distributed cells of VP. In Trichosurus and Dasyurus there is a clear division of VP into dorsomedial (VPM) and ventrolateral (VPL) segments, with the former displaying a higher cell density. This division is evident throughout most of the anteroposterior extent

of VP in Trichosurus but cannot be seen in the caudal half of the nucleus in Dasyurus. In Didelphis it is only occasionally possible, and then with some difficulty, to identify the two divisions of VP in the rostral part of the nucleus. For the most part however the nucleus appears to be structurally homogeneous.

In most but not all of our Trichosurus thalami a further posteromedial subdivision of VP (VPP) can be seen related to the medial aspect of VPM. This region varies in distinctiveness, and also sometimes in location, but is distinguished from adjacent nuclei by the larger size of its constituent neurons (Haight and Neylon 1978c). To date the nucleus has been identified only in Tasmanian representatives of the species, or groups of mainly Tasmanian origin. Rockel et al's (1972) study of the Trichosurus thalamus used animals obtained in New Zealand, where the species is introduced and mostly derives from Tasmanian stock (Pracy 1974). Their illustrations of thalamic cytoarchitecture include a picture of an obvious VPP (their fig. 4 - region designated as VM). On the other hand Golby's (1941) detailed examination of the cytoarchitecture of the Trichosurus thalamus, which was based on South Australian animals, contains no mention or illustration of such a cell group. No equivalent region was detectable in our Dasyurus or Didelphis material, nor have other descriptions of the Didelphis

thalamus (Bodian 1939, Oswaldo-Cruz and Rocha-Miranda 1967) made any mention of such a structure. Examination of the thalami of a number of other Australian marsupials (species listed in descriptions of submedius nucleus (see below)) revealed a possible, though relatively very indistinct, VPP in only one other animal, the wallaby Macropus eugenii. It must be stated, however, that only a limited number of representatives of most species were available for inspection. In view of the variability exhibited by the nucleus in Trichosurus it is possible that examination of larger samples may reveal other animals which possess a distinct VPP. At present, though, the evidence suggests that the cell group is primarily a peculiarity of certain Trichosurus populations.

VM is present throughout most of the rostrocaudal extent of the ventral complex, and is basically similar in the three marsupials. It appears rostrally as a wedge of cells extending from the midline over the medial and dorsal surfaces, firstly of VA, and then more caudally of VL, separating these nuclei from the central intralaminar complex. The caudal part of the nucleus has a similar relationship to VP and is bordered laterally by PO. The boundary between VM and PO is indistinct. VM in Didelphis meets and merges with its fellow on the midline (nucleus interventralis

of Oswaldo-Cruz and Rocha-Miranda 1967), however in the two Australian species the two nuclei remain separate.

The treatment of VM in different studies of the marsupial thalamus varies considerably, and requires some discussion. In Didelphis Bodian (1939) described a ventromedial nucleus, however this cell group probably corresponds to the submedius nucleus of Dasyurus and various placental species (see below). Later, Oswaldo-Cruz and Rocha-Miranda (1967) included Bodian's VM in a larger ventromedial nucleus, which otherwise corresponds closely to VM in Trichosurus and Dasyurus, and to what could be clearly seen to be an equivalent region in our Didelphis material.

Goldby (1941) in his description of the Trichosurus thalamus, did not recognise a ventromedial nucleus, however in a later study (Golby 1943) he redesignated the caudal part of AM as the ventromedial nucleus, to correspond to Bodian's Didelphis VM. As previously discussed (see Anterior Nuclei) we have, on both cytoarchitectural and connective grounds, reinstated this region as part of AM. Rockel et al's (1972) treatment of the Trichosurus VM is essentially the same as our own (Haight and Neylon 1978a), however they included VPP within VM. (See their figure 4 - region designated VM).

In Dasyurus the region we have named submedius nucleus (Haight and Neylon 1981a) is a very distinctive feature of the thalamus. SM first appears rostrally between the ventromedial border of AM and the subparataenial nucleus, the latter of which it replaces at more caudal levels. The nucleus is coextensive with VL, and except for its rostral pole and ventral surface, is surrounded by VM. SM is easily distinguished from VM by its slightly smaller and more closely packed cells.

The Dasyurus SM is identical in appearance and location to the equally prominent cell group in Didelphis which Bodian (1939) referred to as 'nucleus ventralis pars medialis' (ventromedial nucleus). As previously stated Oswaldo-Cruz and Rocha-Miranda (1967) included Bodian's nucleus within their more extensive ventromedial nucleus.

There is substantial justification for separation of these cell groups from the ventromedial nucleus in Didelphis and Dasyurus, and for the application of the term 'submedius' to them. Firstly, apart from the obvious cytoarchitectural distinctiveness of the regions in both species, the Dasyurus SM does not share VM's cortical projections (Haight and Neylon 1981b). Secondly, parallels can be drawn between these nuclei and the submedius nucleus of placental species, in

terms of position and cortical projection fields.

In the rat the terms 'medioventral' (Gurdjian 1927) and 'gelatinosus' (Krieg 1944, Herkenham 1979) have been applied, however most workers (e.g. Craig and Burton 1981, Jones and Leavitt 1974, Krettek and Price 1977a, Lund and Webster 1967a, b) now use the term 'submedius' to refer to a cell group with very similar structure and location to the regions in question in Dasyurus and Didelphis. A submedius nucleus, similar to that in the rat, is also present in carnivores (Ingram et al 1932, Niimi and Kuwahara 1973, Rioch 1929) and primates (Niimi and Kuwahara 1973, Simmons 1980, and see medioventral nucleus of Le Gros Clark 1932). Papez (1932) referred to a submedius nucleus in the armadillo, however his description and figures suggest this is probably more comparable to the subparataenial nucleus of Didelphis and Dasyurus, while rostral parts of his ventromedial nucleus may be equivalent to the SM of these and the other species mentioned above.

No homologue of the Didelphis and Dasyurus SM could be identified in Trichosurus, although on casual examination the caudal part of AM appears to be very similar (compare for example Haight and Neylon 1978a figure 5 with Haight and Neylon 1981a figure 5). In fact Goldby (1943) considered this part of AM to be equivalent to Bodian's VM (=SM) in Didelphis.

Examination of the thalami of numerous other Australian marsupials revealed a distinct SM in several polyprotodont species (marsupial mice, Antechinus swainsonii and Sminthopsis leucopus; Tasmanian devil Sarcophilus harissii; bandicoots, Perameles gunii and Isoodon obesulus), and in two of the less advanced diprotodonts (rat kangaroo, Potorous tridactylus and bettong, Bettongia gaimardi). An SM was not recognisable in more advanced diprotodonts (wallaby, Macropus eugenii, kangaroo, Macropus giganteus, ringtailed possum, Pseudocheirus peregrinus, wombat, Vombatus ursinus), whose thalami closely resemble that of Trichosurus, including the presence of a prominent caudal part of AM.

2. CONNECTIONS AND FUNCTIONS OF THE VENTROPOSTERIOR AND VENTROLATERAL-VENTROANTERIOR COMPLEXES

(a) VENTRO POSTERIOR NUCLEUS - MEDIAL AND LATERAL DIVISIONS

(i) SUBCORTICAL AFFERENT CONNECTIONS

Placentals

The placental VP complex is similarly organised in the

species examined to date. On a purely anatomical basis it is divisible into a (ventro)lateral segment (VPL) which receives spinal cord and dorsal column lemniscal projections, and a (dorso)medial segment (VPM) which receives connections from the principle and caudal divisions of the trigeminal sensory nucleus. In some animals VPL and VPM are recognisable only on the basis of the segregation of these connections, whilst in others a corresponding cytoarchitectural distinction is evident. The great majority of the input connections originate on the opposite side of the cord or medulla. Spinal and dorsal column lemniscal projections overlap extensively in VPL in less advanced species, however there is some evidence for a tendency towards segregation in monkeys. In all cases where spinal and dorsal column lemniscal projections to VPL have been directly compared in a particular animal, the latter have shown by far the greater density. (Spinal projections: rat, Lund and Webster 1967b; cat, Berkley 1980, Craig and Burton 1979; prosimian (Galago), Pearson and Haines 1980a; monkeys, Berkley 1980, Boivie 1979: dorsal column lemniscal projections; rat, Feldman and Kruger 1980, Lund and Webster 1967a; cat, Berkley 1980, Jones and Burton 1974; monkeys, Boivie 1978, Kalil 1981: trigeminal projections: rat, Erzurumlu and Killackey 1980, Feldman and Kruger 1980, Lund and Webster 1967b, Smith 1973; cat, Berkley 1980, Burton et

al 1979; monkeys, Ganchrow 1978, Smith 1975. See also Jane and Schroeder 1971, Schroeder and Jane 1971 for information on hedgehog and tree shrew and Welker 1973 for summary of structure, functions and connections of VP in different mammals and review of earlier literature).

Electrophysiological mapping studies in various species (Jones and Friedman 1982, Jones et al 1982, Loe et al 1977, and see Welker 1973 for review of earlier literature) have shown that somesthetic information from the body projects to VPL, while that from the head projects to VPM. These connections are mostly organised in an orderly manner, with adjacent body or head regions usually being represented in adjacent parts of their respective nuclei. The lower body is generally related to the ventral and lateral, or external, parts of VPL, with the upper body projecting more dorsomedially. Caudal parts of the head project laterally, and the muzzle and mouth regions medially in VPM. Specific body and head regions project to longitudinal cell columns, with most regions being represented throughout much of the rostrocaudal extent of the nuclear complex. Most connections to VP are strictly contralateral although some species also have significant ipsilateral inputs from the mouthparts and certain other midline regions.

Each half of the body and head,then,connects in three dimensions to VP. In the coronal plane the connection pattern can be crudely represented in the form of an upright animunculus, usually with distorted proportions of certain body and head parts, depending on the cross sectional area of the complex occupied by their projections. This distortion presumably reflects the relative peripheral sensory innervation densities in different body regions, and can generally be related to the relative importance of these regions in the animals normal activities. For example, in the raccoon projections from the forepaw occupy much of VP (Welker and Johnson 1965). In some animals such as the sheep, multiple representation of particular specialised body regions, in this case the mouthparts, may be present (Cabral and Johnson 1971).

VP units are characterised by their short latency responses to mechanical stimulation, their relatively restricted and constant receptive fields, and modality specificity. In the monkey there is some evidence for segregation of superficial and deep receptor projections in different parts of VPL (Jones and Friedman 1982, Loe et al 1977).

Marsupials

The anatomical and physiological data available indicate that, in terms of the organisation of input connections,VP in marsupials conforms closely to the general mammalian plan. Rockel et al (1972) examined projections from the dorsal column nuclei and spinal cord in Trichosurus using the degeneration method. Both sets of connections terminate throughout VPL, with a higher density seen in those from the dorsal column nuclei. There was some evidence for a somatotopic organisation of spinal projections. Lesions of the lower cord produced degeneration in ventrolateral, or external VPL, while higher lesions also produced degeneration in the dorsomedial part of this division. No sensory map is available for VP in Trichosurus, however this differential distribution of upper and lower cord projections to VPL indicates a body representation basically similar to that seen in placental species (see above). Rockel's group did not specifically examine trigeminal projections, however their lesions of the dorsal column nuclei involved parts of the spinal trigeminal nucleus, and produced some degeneration in VPM.

In Didelphis VPM and VPL are not easily distinguished on cytoarchitectural grounds, however projections from the spinal cord (Hazlett et al 1972, Mehler 1969) and

dorsal column nuclei (Walsh and Ebner 1973) terminate in the ventrolateral part of VP, while trigeminal projections terminate separately in the dorsomedial part (Walsh and Ebner 1973).

In both Didelphis and Trichosurus these projections exhibit the same predominant laterality as those in placental animals.

Electrophysiological mapping studies of the Didelphis VP have shown that the body and head projection patterns conform to the general organisation seen in placental species, and that the response characteristics of the neurons are very similar. In these studies units were almost exclusively contralaterally driven, and most responded to light mechanical stimulation of the body surface (Bombardieri et al 1975, Pubols and Pubols 1966, Sousa et al 1971). According to Sousa et al (1971), there is an apparent paucity of units activated by deep receptor stimulation in this species compared to placental animals, and those that they located responded primarily to caudal body stimulation. No units activated by joint movements were found by these authors.

(ii) CORTICAL RELATIONSHIPS

Placentals

In the placental species examined to date VP connections can be seen to be organised along similar lines. In the rat and cat,and the prosimian Galago, retrograde HRP tracer studies have shown that specific loci in primary sensory cortex receive projections from longitudinal cell columns or laminae in VP, and that there is a close correspondence between the positions of these laminae and the somatotopic organisation of sensory projections at thalamic and cortical levels (rat, Saporta and Kruger 1977; cat, Kosar and Hand 1981, Saporta and Kruger 1979; Galago, Pearson and Haines 1980b).

In monkeys, the picture is complicated by the segregation of cutaneous and deep receptor projections in different parts of VP (Jones and Friedman 1982, Loe et al 1977), and the further subdivision of these projections at the cortical level, resulting in multiple sensory representations, each corresponding to a distinct cytoarchitectural zone (Kaas et al 1979, Merzenich et al 1978, Nelson et al 1980). While there is some disagreement between authors as to precisely which region of thalamus and cortex comprise VP and the primary somatosensory area respectively, there is

consensus that the two cutaneous receptor projection fields in the cortex (areas 3b and 1) are related to longitudinal columns of cells in the cutaneous zone or core of VP, in a pattern corresponding to the known somatotopic organisation in these regions (Friedman and Jones 1981, Jones and Friedman 1982, Lin et al 1979, Nelson and Kaas 1981, Whitsel et al 1978). Some parts of VP then apparently project to two separate regions within the primary somatosensory area. These projections probably arise from separate neuron populations (Jones et al 1979). The deep receptor zone of VP connects to at least one (area 3a), and probably both (areas 3a and 2), of the deep receptor projection fields of cortex, which are considered by some authors as integral parts of the primary somatosensory area (Friedman and Jones 1981, Jones and Friedman 1982).

In the cat VP also projects in an orderly pattern to the second somatosensory area. Some individual neurons project to both primary and secondary areas (Jones 1975b, Jones and Powell 1969, Spreafico et al 1981).

In the cat and monkey VP receives descending projections from sensory cortex which are in register with the pattern of ascending connections (Jones and Powell 1968, Jones et al 1979).

VP projections in placentals are distributed primarily to layer IV of somatosensory cortex, to adjacent parts of layer III, and to a lesser extent to layer I and upper layer VI (hedgehog, Killackey and Ebner 1972; rat, Herkenham 1980; cat, Jones and Powell 1969; monkeys, Jones 1975a, Jones and Powell 1970).

Marsupials

The early retrograde degeneration studies of Bodian (1942) in Didelphis, and Goldby (1943) in Trichosurus, outlined the overall cortical projection zones of VPL and VPM in the parietofrontal areas of these species, and in the case of Goldby's study provided some evidence of internal organisation in VPL connections.

Later investigations of thalamocortical relationships in Didelphis, using retrograde and anterograde degeneration methods, supply no further information on the areal distribution of cortical projections from different parts of the VP complex (Diamond and Utley 1963, Killackey and Ebner 1972, 1973, Pubols 1968), however recent applications of the retrograde HRP tracer technique in Didelphis (Donoghue and Ebner 1981a, Robards and Ebner 1977), Trichosurus (Haight and Neylon 1978b), and also Dasyurus (Haight and Neylon 1981b), provide details which indicate very close similarities among these species, and a number of

parallels with placental animals. Since the most detailed information available is that for Trichosurus this animal will be used as the basis for comparison.

Injection of HRP into different parts of the parietofrontal area in Trichosurus almost invariably produced columns of labelled cells running through most or all of the rostrocaudal extent of VP, and in some cases extending rostrally into VL. These columns maintained a very constant mediolateral and dorsoventral position. VPL was found to project to the medial, and VPM to the lateral parts of the parietofrontal area (fig 5), corresponding to the body (trunk and limbs), and head somatosensory representation zones respectively, as outlined by electrophysiological mapping studies (Haight and Weller 1973, and see Haight and Neylon 1978b figure 1).

Within the body area there was an extremely precise correspondence between the locations of cortical injections and label columns in VPL. Injections in caudal parts of the cortex (trunk area) produced label in lateral (dorsal) VPL, while progressively more rostral injections (limb areas) produced label in progressively more medial (ventral) parts of the nucleus. In addition, injections along the medial cortical margin (caudal trunk and hindlimb areas)

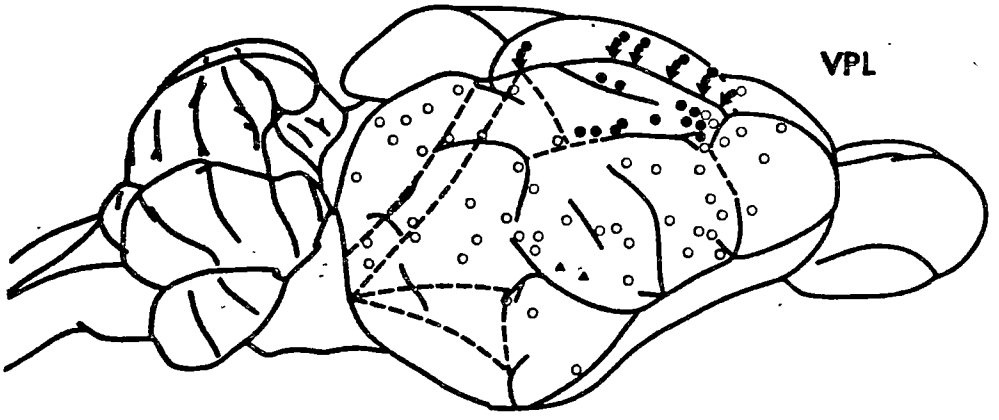
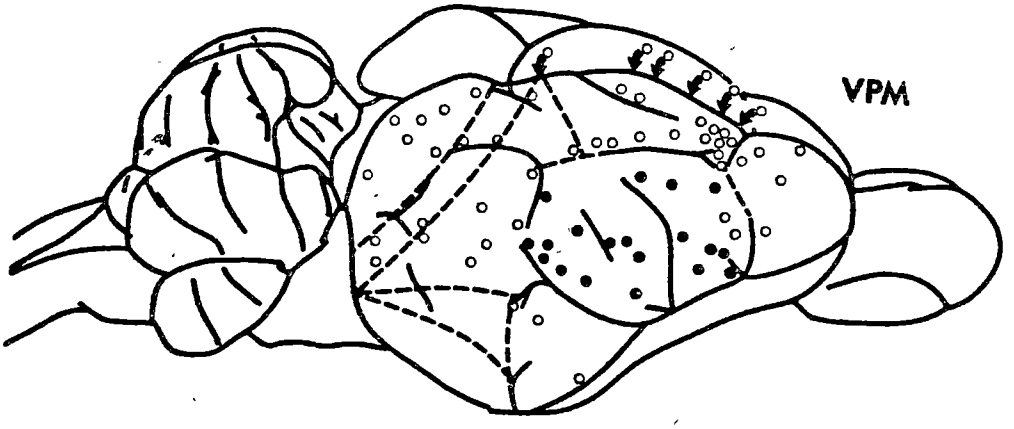


Figure 5

A. Cortical HRP injection in Trichosurus which produced retrograde label in the lateral division of the ventroposterior nucleus (closed circles).



B. Cortical HRP injection which produced labelling of the medial division of the ventroposterior nucleus.

(For further details see Haight and Neylon 1978b).

produced label mostly confined to a ventral and lateral, or external, layer of VPL, while more laterally placed injections (rostral trunk and forelimb areas) labelled dorsomedial or internal parts of the nucleus (Haight and Neylon 1978b figures 8 and 9). These findings strongly suggest a three dimensional representation of the body in VPL very similar to that reported for many placental species, and for Didelphis (Pubols and Pubols 1966, Sousa et al 1971, Welker 1973 for review of placental species), and is in keeping with the evidence for segregation of rostral and caudal spinal cord projections to the nucleus seen in the study of Rockel et al (1972).

VPM projections to the lateral parietofrontal area displayed a somewhat different organisation. Label fields in VPM appeared in the same columnar form as seen in VPL, however these were not restricted to internal or external layers of the nucleus. Shifts of label columns from lateral (dorsal) to medial (ventral) parts of the nucleus were in this case related to sequences of injection placements radiating rostrally, or rostrolaterally, from the caudomedial margin of the head area. In addition, VPM dislayed a second smaller projection field at the rostrolateral margin of the parietofrontal area, where a lateral to medial shift of label columns in VPM with progressively more rostral cortical injections was repeated (see Haight and Neylon

1978b figs 10-13 for details).

This dual VPM projection presents some interpretative problems. The results indicate that specific regions of the nucleus project to separate areas of cortex, which, on the presently available evidence, receive sensory connections from different parts of the head (see Haight and Neylon 1978b, figure 1). This may reflect an extremely complex organisation of head sensory projections at the thalamic level, however an alternative answer would be the presence of a duplicate representation of certain head structures, in the area corresponding to the smaller rostral VPM field. Electrophysiological mapping, however, has so far provided no evidence for multiple representations of any part of the body or head in the primary sensory cortex in Trichosurus, although the region in question has not been examined intensively. Resolution of this problem must await further careful mapping of this region, and of VPM.

The organisations of VPM and VPL projections, then, exhibit some important dissimilarities, perhaps reflecting major differences in the complexity and distortion of somatotopy in the two nuclei, and in their respective cortical projection fields.

Both VPM and VPL were found to project to a small caudolaterally placed part of the parietofrontal area, corresponding to the position of the second somatosensory area as determined by electrophysiological mapping (Haight and Weller 1973 and unpublished observations).

Our Dasyurus HRP study (Haight and Neylon 1981b) provides relatively limited details of the VP projection pattern, however the separation of VPL and VPM projections to medial and lateral parts respectively of the parietofrontal area, the appearance of columns of retrogradely labelled cells extending throughout most of the rostrocaudal extent of these nuclei, and the correlation between caudal to rostral sequencing of injection sites, and lateral (dorsal) to medial (ventral) shifts in thalamic labelling, all indicate close similarities between this species and Trichosurus.

In neither Dasyurus or Trichosurus does the VP(L) projection field include the extreme rostromedial margin of the parietofrontal area. The significance of this finding will be discussed at a later point.

In Didelphis, the region designated by Donoghue and Ebner (1981a) as the external division of VB (= VPL) was shown to project in an orderly manner to the large forelimb area of cortex, while their arcuate division

of VB (=VPM) projects to the face region. As with Trichosurus and Dasyurus caudal areas of the cortex are related to dorsal (lateral), and rostral areas of cortex to ventral (medial) parts of VP. Their cortical HRP injections produced longitudinal columns of labelled cells which extended throughout much of the rostrocaudal extent of the appropriate VP divisions, and continued rostrally into VL.

The second somatic sensory area in the animal has also been shown to receive organised connections from VPL (Robards and Ebner 1977).

Thus, in Didelphis there is a clear correlation between the pattern of VP projection to cortex, as demonstrated with anatomical methods, and the cortical and thalamic sensory representations as outlined by electrophysiological mapping studies (Lende 1963a, Pubols and Pubols 1966, Pubols et al 1976, Sousa et al 1971).

Didelphis possesses a double cortical representation of the mystacial vibrissae and rhinarium (Pubols et al 1976), yet within VP only a single representation has been reported (Bombardierie et al 1975, Pubols and Pubols 1966, Sousa et al 1971). Presumably the anatomical basis for this cortical organisation is a double projection from parts of VPM, perhaps along similar lines to the apparent dual projection of VPM

seen in Trichosurus.

In Trichosurus and Didelphis VP connections to the primary somatosensory area show strict reciprocity (Donoghue and Ebner 1981a, Haight et al 1983).

Nothing is known of the laminar distribution of VP's cortical connections in Trichosurus or Dasyurus, however in Didelphis these terminate mostly in layer IV and adjacent parts of layer III, and to a lesser extent in layer I and upper layer VI (Donoghue and Ebner 1981b, Killackey and Ebner 1972).

Summary of Cortical Relationships and Comparison of Placental and Marsupial Organization

The organization of VP connections with the somatosensory cortex is basically similar in all the mammalian species examined to date. Specific areas of cortex are related reciprocally, and in an orderly manner, to columns or laminae of cells oriented longitudinally in VP. The ordering of projections shown by anatomical methods correlates well with what is known of the somatotopic organisation of somesthetic projections, as determined by electrophysiological mapping at thalamic and cortical levels.

VP projects to both the primary and secondary somatosensory areas of cortex, and in monkeys, Trichosurus, and probably in Didelphis, it appears that specific parts of VP may have dual projections to separate parts of the primary area.

The laminar distribution of VP projections to cortex is very similar in all the mammals for which information is available.

(b) VENTROPOSTERIOR NUCLEUS - PARVOCELLULAR AND PRINCIPLE DIVISIONS

The search for possible homologues and functions of the Trichosurus VPP presents some difficulties. As stated previously, the nucleus has so far only been identified with any real degree of certainty in this species among the marsupials, and it may in fact be limited to a particular subgroup of the species. On the basis of appearance and location there is a strong temptation to equate VPP with the parvocellular division of VPM (VPMpc) of placental species such as the cat (Rinvik 1968a) and rhesus monkey (Olszweski 1952), although the nuclei differ in the relative sizes of their constituent neurons. VPP neurons are uniformly larger than those of any adjacent nucleus (Haight and Neylon 1978c), which is not the case with the cat and monkey VPMpc.

Connections and Possible Functions of VPMpc and VPP

Some studies in placental species have considered that VPMpc is more appropriately included as part of VM, however despite differences in nomenclature it is clear that this region receives ascending gustatory and lingual projections, which are then relayed to the rostrolateral margin of the parietal area, adjacent to the rhinal fissure (rat, Emmers et al 1962, Ganchrow

and Erickson 1972, Norgren and Leonard 1973, Norgren and Wolf 1975, Saper and Loewy 1980, Wolf 1968, Yamamoto et al 1980; rabbit, Yamamoto and Kawamura 1975; cat, Ruderman et al 1972; primates, Beckstead et al 1980, Blomquist et al 1962, Ganchrow and Erickson 1972).

In their study of thalamic afferent connections in Trichosurus, Rockel et al (1972) described an experiment in which a medullary lesion produced, in part, a small contralateral focus of dense degeneration adjoining the medial part of VPM. This degeneration field could possibly correspond to the location of VPP (see their fig 7 expt. 16 and compare with Haight and Neylon 1978c fig 9). Rockel's group considered this result to be indicative of a solitary nucleus (gustatory) projection to the region. The presence of a gustatory input to VPP would clearly provide strong grounds for considering the nucleus as equivalent to the placental VPMpc.

Other considerations, however, leave these authors' conclusions in some doubt. Firstly, direct contralateral solitariothalamic projections have not, as far as is known, been demonstrated in other species. In the cat no direct connections are evident (Morest 1967), and in the rat gustatory information reaches the thalamus via connections with the parabrachial nucleus

(Norgren and Leonard 1973, Saper and Loewy 1980). In the cynomolgus monkey, direct solitary nucleus connections terminate almost exclusively in the ipsilateral VPMpc (Beckstead et al 1980).

Furthermore, in the experiment in question in the study by Rockel's group, involvement of other medullary centres by this lesion allows for alternate interpretations of the results, including the possibility of a trigeminal projection to the medial portion of the posterior nucleus (see Neylon and Haight 1983).

Thus, although the data presented by Rockel et al are, on initial examination, very suggestive of a close similarity between VPP and the placental VPMpc, their results, and their interpretation of these results, must be seen as inconclusive.

The cortical connections of VPP remain to be considered. From careful comparison of these connections with those of VPMpc, it is apparent that despite their rather compelling superficial similarities, the nuclei are not equivalent structures.

VPP projects to a region of cortex at the rostral margin of the lateral parietofrontal area, some

distance from the rhinal fissure (Haight and Neylon 1978b and see fig 6). Electrophysiological investigations have shown that this region receives connections from mechanoreceptors in the lips and intraoral structures, excepting the tongue (Haight and Weller, unpublished observations). This information is presumably relayed to the cortex, in part at least, by VPP. In Didelphis, the lips and most intraoral structures are represented in a similarly located area of cortex to Trichosurus, while tongue information projects more rostrally and laterally, to an area nearer the rhinal fissure (Pubols et al 1976). The tongue projection in Trichosurus has yet to be located, however it seems reasonable to expect it to be placed as it is in Didelphis, since with the important exception of a dual representation of the mystacial vibrissae and rhinarium in Didelphis, but not Trichosurus, the cortical sensory maps of the two animals are basically similar (Haight and Weller 1973, Lende 1963a, Pubols et al 1976).

The placental gustatory and lingual (VPMpc) projection field would appear to correspond reasonably well in location to the Didelphis, and hence also perhaps the Trichosurus, tongue representation (rat, Ganchrow and Erickson 1972, Norgren and Wolf 1975, Wolf 1968, Yamamoto et al 1980; rabbit, Yamamoto and Kawamura 1975; marmoset, Ganchrow and Erickson 1972).

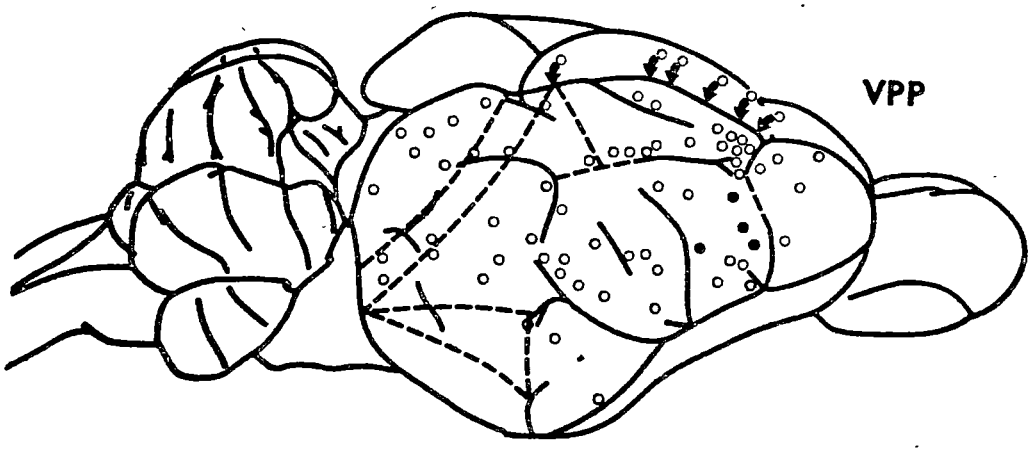


Figure 6

Cortical HRP injection in Trichosurus which resulted in retrograde labelling of the principal division of the ventroposterior nucleus (closed circles).

(For further details see Haight and Neylon 1978b).

In the cat, VPMpc connects to an area of cortex rostral and lateral to, and separate from, the projection field of medial parts of VPM, which receive information from the mouthparts, excepting the tongue (Ruderman et al 1972). Thus, there would appear to be reasonable grounds for considering that the Trichosurus VPP and placental VPMpc convey different kinds of information to differently located areas of cortex.

Furthermore, gustatory and lingual projections to the placental VPMpc and cortex have been shown to have strong ipsilateral or bilateral components (rat, Ganchrow and Erickson 1972, Norgren and Leonard 1973, Saper and Loewy 1980, Yamamoto et al 1980; rabbit, Yamamoto and Kawamura 1975; cat, Ruderman et al 1972; primates, Beckstead et al 1980, Benjamin and Burton 1968, Benjamin et al 1968, Blomquist et al 1962, Ganchrow and Erickson 1972), and it seems likely that a similar arrangement for such connections would be present in marsupials. On the other hand, the projections from the lips and mouthparts to the cortex (presumably in part at least via VPP) in Trichosurus, appear to be strictly contralateral, as is the case with Didelphis (Haight and Weller, unpublished observations, Pubols et al 1976).

From the above then it would appear that, not only do the Trichosurus VPP and placental VPMpc probably relay different kinds of information, but that their projections also differ significantly in laterality and in the locations of cortical terminal fields. These factors, together with the evidence for differences in the internal structure of the nuclei, strongly suggest that VPP and VPMpc are not homologous structures, despite their superficial similarities. The concurrence of the areas of cortex shown by anatomical methods to receive VPP projections, and by physiological methods to receive lip and mouthpart projections, indicates that VPP may be a specialised trigeminal relay centre.

(c) VENTROANTERIOR AND VENTROLATERAL NUCLEI

(i) SUBCORTICAL AFFERENT CONNECTIONS

While the sources of the major afferent connections of the rostral ventral tier nuclei are common to all the mammals examined so far, it is difficult to make detailed interspecies comparison of the organisation of these connections. Limited data are available for marsupials, and among placentals research has focused upon a restricted number of species, i.e. the rat, cat and monkeys. In examining the literature one is faced with varying systems of nuclear subdivisions and

nomenclature in different animals, the failure in some cases of major afferent pathways to respect recognised nuclear boundaries, and the existence of important interspecies differences in the distribution, extent, and degree of overlap of the principal inputs. These factors can make it extremely difficult to recognise homologous regions in different animals.

Placentals

The main projections to the VA-VL complex in placentals have long been recognised to be those from the cerebellum and medial pallidal segment (or entopeduncular nucleus of nonprimates). In some animals at least, the substantia nigra and spinal cord also have important inputs to this region. The ventromedial nucleus shares some of these connections, and in view of the difficulties outlined above in comparing these parts of the ventral nuclear group in different species, the organisation of the cerebellar, pallidal and nigral inputs to VM will also be considered here. A more detailed examination of VM connections will be presented at a later stage.

The rat is probably the best animal to use as a basis for comparison, since cerebellar, entopeduncular nucleus (EPN), and nigral projections have all been examined in this species, and these relate fairly

closely to the relatively simple and uniform system of nuclear parcellation applied by different authors to the parts of the thalamus in question. The rat VM is considered to be the sole recipient among the ventral group of nigral projections (Beckstead et al 1979, Clavier et al 1976). VA and VL are not recognised as separate nuclei, and the VA-VL complex, with the possible exception of a small region at the rostral pole, receives massive cerebellar connections, as does VM (Donoghue et al 1979, Faull and Carman 1978, Haroian et al 1981). The EPN is strongly connected to ventromedial parts of the VA-VL complex, and to the lateral margin of VM (Carter and Fibiger 1978). The EPN and nigral terminal fields, then, are totally contained within that for the cerebellum.

The cat and monkey are difficult to compare with each other or with the rat. In the cat there is a basic disagreement between authors as to the distribution of cerebellar projections to ventral tier nuclei. Hendry et al (1979) reported that cerebellar fibres terminate only in dorsolateral parts of VA and VL, and not in VM. Other studies, however, indicate a projection field extending throughout VA, VL and VM (Angaut and Bowsher 1970, Kievit and Kuypers 1972, Sugimoto et al 1981). The reason for this discrepancy is not clear. If the weight of evidence is accepted, however, the cat would

appear to be comparable to the rat, except in the matter of the apparent inclusion of all parts of the VA-VL complex in the cerebellar projection field. As with the rat, projections from the cat EPN terminate in ventromedial parts of the VA-VL complex, and also in lateral VM (Hendry et al 1979, Larsen and McBride 1979). Nigral connections, however, differ from the rat, in being distributed to ventromedial parts of the VA-VL complex, as well as to VM (Hendry et al 1979).

Again, if one accepts the weight of evidence with respect to the cerebellar projection field in the cat, this totally overlaps those for the entopeduncular nucleus and substantia nigra, as in the rat.

A small, ill defined region at the caudal margin of VL, adjacent to VP, has been shown to receive, in addition to cerebellar connections, projections from the spinal cord in the cat (Berkley 1980, Jones and Burton 1974). According to Berkley (1980), this transition or border zone of VL also receives inputs from the dorsal column lemniscal pathway, however Jones and Burton (1974) found that such projections do not extend beyond what they considered to be the rostral boundary of VP.

Most studies of primate thalamic projections follow the complex systems of nuclear subdivision and nomenclature devised by Walker (1938) and Olszweski (1952) for the

rhesus monkey (and see recent reexamination of ventral tier cytoarchitecture in monkeys by Asanuma et al 1983a). These authors did not recognise a VM, and divided the ventral tier into numerous subnuclei. Projections from the cerebellum in monkeys have been shown to terminate in most centres rostral to the caudal division of VPL (VPLc), which is the principal dorsal column lemniscal relay centre. The exceptions are two small medially placed cell groups, the magnocellular division of VA (VAmc), and the medial division of VL (VLm). The cerebellar projection field then encompasses the regions usually designated as: the oral division of VPL (VPLo), also known as the ventrointermediate nucleus (Vim), the caudal and oral divisions of VL (VLc and VLo respectively), the parvocellular division of VA (VApc), and nucleus X (Asanuma et al 1983b, Kalil 1981, Kievit and Kuypers 1972, Miller and Strominger 1977, Tracey et al 1980).

The internal pallidal segment is heavily connected to VLo and VApc, and also lateral VLm, but not to VAmc, or nucleus X. There is some disagreement over the possibility of a relationship with VLc, however, if present, this is probably relatively insignificant (De Vito and Anderson 1982, Kim et al 1976, Kuo and Carpenter 1973, Nauta and Mehler 1966). Thus, once more the pallidal projection field lies totally within that

of the cerebellum.

Nigral projections are apparently restricted to VAmc and VLm in the rhesus monkey (Carpenter et al 1976). This would suggest that these regions are homologous to the rat, and possibly the cat VM, although unlike these animals, they do not receive any cerebellar connections.

VPLo (Vim), the caudal most division of the VA-VL complex, receives a significant spinal input in the prosimian Galago (Pearson and Haines 1980a, 1981) and monkeys (Asanuma et al 1983b, Boivie 1979, Tracey et al 1980). This region, then, may be equivalent to the 'spinal' part of VL in the cat. It seems clear that VPLo in monkeys does not receive any connections from the dorsal column nuclei (Asanuma et al 1983b, Berkley 1980, Boivie 1978, Kalil 1981, Tracey et al 1980).

Principal Similarities and Differences Among Placental Mammals

The common factors evident in the placental animals studied so far are then, firstly that the cerebellum has by far the most extensive connections within the rostral ventral tier nuclei, with relatively restricted distributions of pallidal (or EPN) and nigral inputs. Thus, large areas of the VA-VL complex receive only

cerebellar fibres. Secondly, that cerebellar projections encompass totally, or almost totally, those from the pallidum, or EPN. And thirdly, that nigral connections show some overlap with those from the pallidum (EPN), this being extensive in the cat, but relatively slight in the rat and monkey. In the cat and primates the caudal most portions of the VA-VL complex receive spinal connections. This spinal field lies within the cerebellar projection zone. No similar organisation has been described in the rat.

Some important differences between these animals are, the overlap of cerebellar and nigral projections in the rat and cat, but not monkeys, and the relatively extensive distribution of nigral connections in the cat compared to the other species.

Marsupials

Nothing is known of the projections of the substantia nigra and pallidum or EPN in marsupials. Rockel et al (1972) described major cerebellar connections to VL, but not to VA or VM in Trichosurus. Walsh and Ebner (1973), and later Martin et al (1974), showed that the Didelphis VA-VL complex receives a similarly massive cerebellar input. It appears from these studies that the rostral extremity of the complex, which may

correspond to VA, is excluded from the cerebellar projection field, thus indicating a similar organisation to that in Trichosurus. On the other hand, a significant input to VM was found by these latter authors, in contrast to the situation reported in Trichosurus.

Nothing is known of the input connections of VA in Trichosurus, and since the cerebellar projection field in Didelphis apparently excludes VA, the same is true for this species.

In neither Trichosurus or Didelphis is there any evidence for significant spinal or dorsal column lemniscal projections to any part of the VA-VL complex (Mehler 1969, Rockel et al 1972, Walsh and Ebner 1973).

Summary of Subcortical Afferent Connections and Comparison of Placental and Marsupial Organisation

In placental animals the rostral ventral tier nuclei receive major projections from the cerebellum, pallidum (or entopeduncular nucleus) and substantia nigra, with those from the cerebellum being by far the most extensive. The precise distribution and degree of overlap of these connections varies somewhat between the species for which detailed information is available, the rat, cat, and monkeys, although certain

general similarities are evident.

Comparison among marsupial species can only be made in terms of cerebellar projections since nothing is known of the organisation of entopeduncular nucleus and nigral pathways in these animals. On the basis of cerebellar connections the VA-VL complexes in Trichosurus and Didelphis are similar, in that the terminal fields in both cases are probably limited to VL. An important difference is seen with respect to VM, however, since on the presently available evidence this nucleus receives cerebellar inputs in Didelphis but not in Trichosurus.

The pattern of cerebellar projections to the VA-VL complexes in Trichosurus and Didelphis is comparable to that seen in the rat, since in this animal the rostral pole of the complex (=VA?) may not receive cerebellar fibres. In the cat and monkey, however, the cerebellar projection fields would appear to be more extensive, involving all, in the case of the cat, or nearly all, in monkeys, of the rostral ventral tier nuclei. Thus, it is not possible at present to compare individually the marsupial VA or VL with specific cell groups in either of these placental animals on the basis of afferent connections. With respect to cerebellar connections to VM, the Didelphis organisation is similar

to that seen in the rat, and according to the weight of evidence, the cat, but differs from monkeys where the possible equivalent(s) to VM (VLm and possibly VAmc) do not receive such projections.

Projections from the spinal cord terminate in caudal portions of the VA-VL complexes (as well as in VP) in the cat and primates. There is some dispute over the possibility that fibres from the dorsal column nuclei also connect to the region in question in the cat (Berkley 1980, Jones and Burton 1974), but monkeys clearly lack any such inputs. No substantial somesthetic pathway projections to the VA-VL complex have been described in the rat or marsupials.

(ii) CORTICAL RELATIONSHIPS

Placentals

In the studies by Donoghue et al (1979) in the rat, and by Pearson and Haines (1980b) in the prosimian *Galago*, it was found that placement of HRP in different parts of the motor (rat), or sensorimotor (rat and *Galago*) cortex (see Hall and Lindholm 1974, Kanagasuntheram et al 1966), produced retrograde labelling of cells which were scattered in the VA-VL complex, rather than grouped into definite foci. In contrast label fields in VP following HRP placement in sensory and

sensorimotor cortex formed compact longitudinal columns, located in general accordance with the somatotopic organisation of body and head sensory projections at thalamic and cortical levels. In these species, then, it would appear that VA-VL projections to cortex are not highly ordered, unlike those for VP. Herkenham (1980), on the basis of results from his anterograde tracer studies in the rat, considered that VA-VL projections are not confined to the motor area, but are distributed, though sparsely, throughout many areas of cortex.

In the cat and monkeys specific locations in motor cortex have been shown to receive projections from longitudinal columns or laminae of VA-VL cells (Hendry et al 1979, Strick 1973, 1975, 1976a). A fairly orderly point to point relationship is evident between VA-VL and cortex, although this is by no means as precisely organised as VP projections to the somatosensory area (Jones et al 1979, Kievit and Kuypers 1977, Strick 1973, 1975, 1976a, and see VP discussion).

The pattern of VA-VL projections in the cat and monkey, as determined anatomically, corresponds to the somatotopic pattern of body part movements elicited by electrical stimulation of specific regions of VA-VL and

motor cortex in these animals (Strick 1973, 1975, 1976a,b).

In the cat the VA-VL complex, though mostly VL, projects heavily to area 4 and adjacent parts of area 6 of the motor cortex, and receives descending projections from these areas (Hendry et al 1979, Strick 1973). Projections have also been reported from parts of VA-VL, though principally VA, to prefrontal (Niimi et al 1981a), limbic (Niimi et al 1978, Robertson and Kaitz 1981), and posterior parietal cortex (Hendry et al 1979, Itoh and Mizuno 1977, Niimi et al 1979, Robertson 1977, Tanji et al 1978). There is some difference of opinion between authors over the extent of cortical projections from the 'spinal' zone of caudal VL, adjacent to VP, which receives inputs from the spinal cord, cerebellum and possibly the dorsal column nuclei (Berkley 1980, Hendry et al 1979, Jones and Burton 1974). Strick (1973) found that this region is connected to area 3a, at the rostral margin of the primary somatosensory area, and included it as part of VP. Larsen and Asanuma (1979), however, have described projections to both area 3a and motor cortex, while Spreafico et al (1981) demonstrated a connection with the secondary somatosensory area, and considered that the region may also project widely to primary sensory cortex. It would seem clear that the remainder of VA-VL does not project to somatosensory cortex (Hendry et

al 1979, Larsen and Asanuma 1979, Spreafico et al 1981, Strick 1973).

VPLo, VLc and VLo in monkeys project heavily to, and in turn receive descending projections from motor cortex (Asanuma et al 1983b, Friedman and Jones 1981, Horne and Tracey 1979, Jones et al 1979, Kievit and Kuypers 1977, Strick 1975, 1976a). The two subnuclei of VA are related to rostral motor cortex, and also to the prefrontal and posterior parietal areas (Carmel 1970, Divac et al 1977, Kasdon and Jacobson 1978, Kievit and Kuypers 1977). A significiant projection from VLc to posterior parietal cortex has also been reported (Kasdon and Jacobsen 1978).

VPLo, which receives both spinal and cerebellar inputs (Asanuma et al 1983b, Boivie 1979, Kalil 1981, Tracey et al 1980), and is thus similar, in this respect at least, to the 'spinal' part of the cat VL, is connected only to motor cortex, and not to area 3a, or any other part of somatosensory cortex. No division of VA-VL has been shown to project to sensory cortex in monkeys (Friedman and Jones 1981, Jones and Leavitt 1974, Jones et al 1979, Strick 1975, 1976a, Tracey et al 1980).

Few studies have examined the laminar distribution of VA-VL projections to cortex in placental animals.

According to Jones (1975a), layer III of motor cortex in the squirrel monkey receives the majority of terminals, with some additional inputs to layer I. Similarly, in the cat, the main input is to lamina III, with minor connections to laminae VI and I (Strick and Sterling 1974). Herkenham (1980) found that layers III and IV were the principal VA-VL projection zones in the rat motor cortex, while in other regions fibres terminated mainly in layers I and VI.

Marsupials

Didelphis

The recent HRP and amino acid tracer study of Donoghue and Ebner (1981a) in Didelphis showed that the VA-VL complex in this animal is connected reciprocally, in a highly ordered manner, to a large extent of the parietofrontal area, and also projects to the posterior parietal and 'post orbital' areas. These authors did not differentiate between the two nuclei, and from their descriptions it would appear that in terms of the organisation of their cortical projections, they are in fact indistinguishable.

Their findings confirm and extend those from earlier retrograde and anterograde degeneration studies in Didelphis (Bodian 1942, Diamond and Utley 1963,

Killackey and Ebner 1973, Martin et al 1975, Pubols 1968).

VA-VL projections to the parietofrontal and 'post orbital' areas overlap extensively those of VP (Donoghue and Ebner 1981a, Killackey and Ebner 1973), except possibly in the region of the second somatic sensory area (Robards and Ebner 1977), and also display a parallel homotypical relationship with cortex. This confirms physiological evidence for a complete overlap and congruence of the motor and primary sensory areas in Didelphid marsupials (Lende 1963a,b, Magalhaes-Castro and Saraiva 1971). Convergence of VA-VL and VP projections occurs even in terms of laminar distribution, since VA-VL projects primarily to layers I, III and IV. The terminal densities in various laminae do, however, differ somewhat for the two sets of connections (Donoghue and Ebner 1981b).

Donoghue and Ebner (1981a) found that injections of tracer into different parts of the parietofrontal area produced overlapping columns of retrogradely and anterogradely transported label which extended through VP and VA-VL, while maintaining relatively constant mediolateral and dorsoventral relationships. Dorsal (lateral) parts of VA-VL (and VP) were shown to be related to the caudal part of the forelimb area

(proximal forelimb representation), which comprises a major part of the medial sensorimotor cortex in this animal. Ventral (medial) parts of the nuclei are related to the rostral forelimb area (distal forelimb representation). Dorsomedial VA-VL and VP are connected to the face region. As noted previously (see VP discussion), the pattern of VP projection to cortex correlates well with the known somatotopic organisation of sensory projections at both thalamic and cortical levels. The congruence of the motor and sensory cortical representations, and parallel patterns of VA-VL and VP projections, implies that VA-VL is somatotopically organised along very similar lines to VP, though in this case with respect to body part movements.

VA-VL projections to the posterior parietal area originated from longitudinal columns of cells in the dorsal part of the complex, while injections of HRP in the 'post orbital' area labelled both VA-VL and VP cells, but these were scattered rather than grouped into columns. These 'post orbital' area injections also labelled MD, indicating a degree of overlap of the sensory motor and prefrontal areas in this animal.

Trichosurus and Dasyurus

The limited data available from our examination of

thalamic projections to the parietofrontal area in Dasyurus (Haight and Neylon 1981b) suggest that this animal is similar to Didelphis in that, although VA and VL are cytoarchitecturally distinct structures, they project to similar regions of cortex. Our findings in Trichosurus show a more complex organisation of VA and VL connections. The distinctions between VA and VL in terms of cytoarchitecture and afferent connections are further reflected in different cortical relationships. In addition, VL is divided into two distinct cell groups, each projecting to different areas of cortex (Haight and Neylon 1977, 1979, Haight et al 1983).

VL Projections

The external division of VL (VLe) in Trichosurus is similar, both in its cytoarchitecture and the organisation of its cortical projections, to the Dasyurus VL. The small internal division of VL (VLi) has so far only been recognised in Trichosurus, where it displays a distinctive pattern of cortical connections.

Our retrograde HRP transport studies have shown that VLe in Trichosurus, and VL in Dasyurus, project in an orderly manner to medial and rostral parts of the parietofrontal area (Haight and Neylon 1979, 1981b and

see fig 7). The distribution of the VLe projections seen in our Trichosurus material corresponds reasonably well with descriptions of the extent of VL projections in earlier retrograde and anterograde degeneration studies in this animal (Goldby 1943, Ward and Watson 1973).

The VLe and VL projection fields in Trichosurus and Dasyurus only partially overlap those of VP (see Haight and Neylon 1979 fig 5, Haight and Neylon 1981b fig 2). Overlap is extensive in the VPL, or body sensory projection area, in the medial part of the parietofrontal area. A small rostral part of the medial parietofrontal area receives projections from VLe/VL but not VP(L). In the VPM field, or head sensory projection area of lateral parietofrontal cortex, VLe/VL projections are restricted to the rostromedial margin. Thus, large parts of the parietofrontal area receive VP(M) projections only, while a small rostromedial zone receives VLe/VL projections only. Our findings are supported by those from various electrophysiological studies, which have shown that in Trichosurus and related diprotodont marsupials a small rostromedial part of the parietofrontal area does not respond to somatosensory stimuli (Haight and Weller unpublished observations, Johnson et al 1973, Weller et al 1977), and that in various Australian marsupials including Trichosurus and

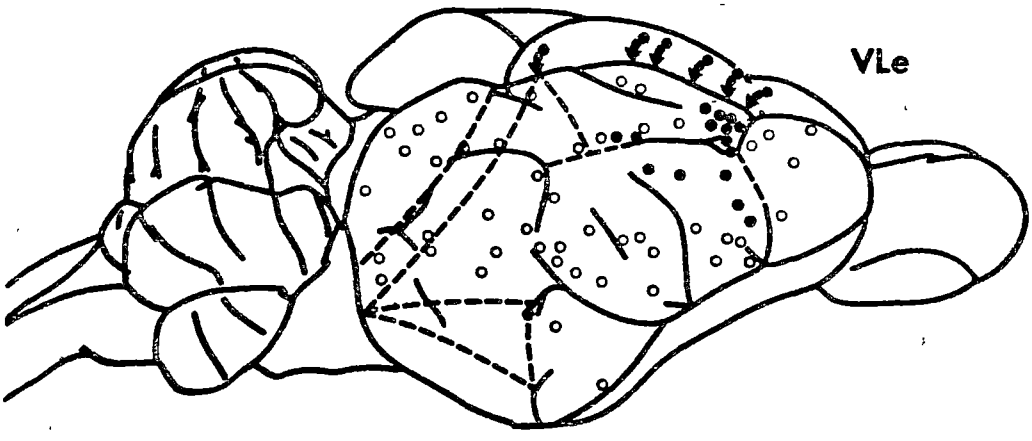


Figure 7

Cortical HRP injections in Trichosurus which produced retrograde labelling in the external division of the ventrolateral nucleus (closed circles).

(For further details see Haight and Neylon 1979).

Dasyurus, electrical stimulation of only the rostromedial part of the parietofrontal area produces discrete body movement (Abbie 1940, Goldby 1939, Rees and Hore 1970).

In our Trichosurus and Dasyurus material it was found that progressive caudal to rostral shifts in the placement of HRP injections in the VLe/VL cortical fields produced corresponding shifts in columns of retrogradely labellel cells from lateral to medial parts of the nuclei. The representation of body movement parts in motor cortex in Trichosurus has not been determined in detail. There is also some discrepancy between the position of the rostral boundary of cortex from which discrete movements can be elicited by electrical stimulation, and the rostral boundary of the VLe field as demonstrated by our anatomical methods. There is, however, general agreement between different physiological studies that stimulation in sequence from caudal to rostral parts of the motor cortex produces, in progression, movements in the hindlimb, forelimb and head (Abbie 1940, Goldby 1939, Rees and Hore 1970). Thus, it can be argued that there may be a somatotopic organisation within VLe such that lateral parts of the nucleus are concerned with movements of the hindlimb, and medial parts with movements of the forelimb and head. This would roughly

approximate the somatotopic organisation of sensory projections in VP, since VPM and internal and external layers of VPL can be related to the relaying of head, upper body and lower body sensations respectively (see VP discussion).

As previously stated, the proximal and distal forelimb representation areas in the Didelphis sensorimotor cortex, and the trunk and limb representations in the Trichosurus sensory cortex, are related to dorsolateral and ventromedial parts of VA-VL (Didelphis) and VPL (Didelphis and Trichosurus) respectively. We could find no comparable organisation with respect to Trichosurus VLe-cortical connections.

In Trichosurus combined HRP and tritiated amino acid injections in cortex produced overlapping columns of retrograde and anterograde labelling in VLe, indicating a strict reciprocity of connections (Haight et al 1983).

In those experiments where both VP and VLe/VL were retrogradely labelled in Trichosurus and Dasyurus, label columns extended through VP and continued rostrally into VLe/VL, while maintaining a relatively constant position, although generally the columns expanded both dorsally and mediolaterally in the latter nuclei. The extensive Trichosurus data provided

evidence for a pattern in VLe projections additional to that described above. HRP injections in lateral parts of the VLe cortical terminal field produced label columns restricted mainly to caudal parts of the nucleus, while more medially placed injections produced columns extending into rostral VLe (see Haight and Neylon 1979, fig 10).

The small internal division of VL (VLi) in Trichosurus is related to the VPM field in the lateral part of the parietofrontal area (fig 8a), and its projections overlap only minimally those of VLe (see Haight and Neylon 1979 fig 4). Some, but not all HRP injections in this region produced very intense retrograde labelling of small groups of cells in VLi. This differs from the situation for VLe, where all injections within the projection field produced less intense labelling of large numbers of neurons. Those injections which did label VLi were found to be located within the area of cortex which contains the barrel field (Weller 1972).

VA Projections

In Dasyurus thalamic projections to only the parietofrontal area have been examined (Haight and Neylon 1981b). Our results suggest that this species

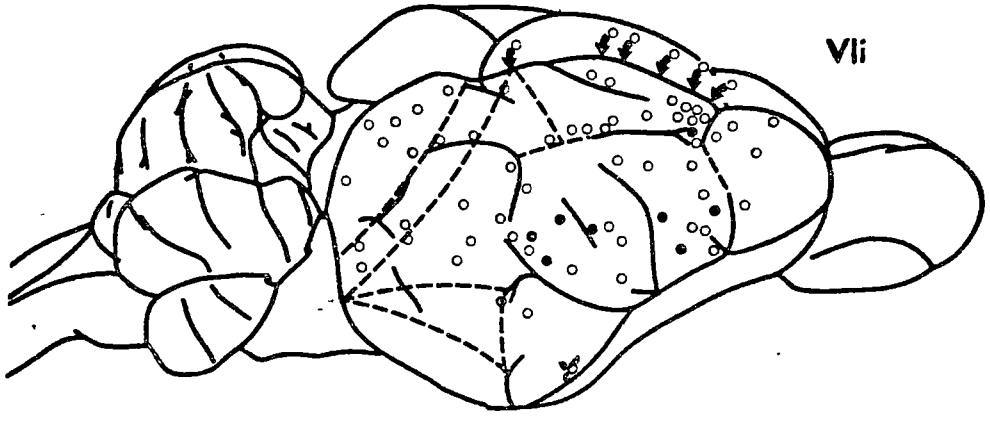
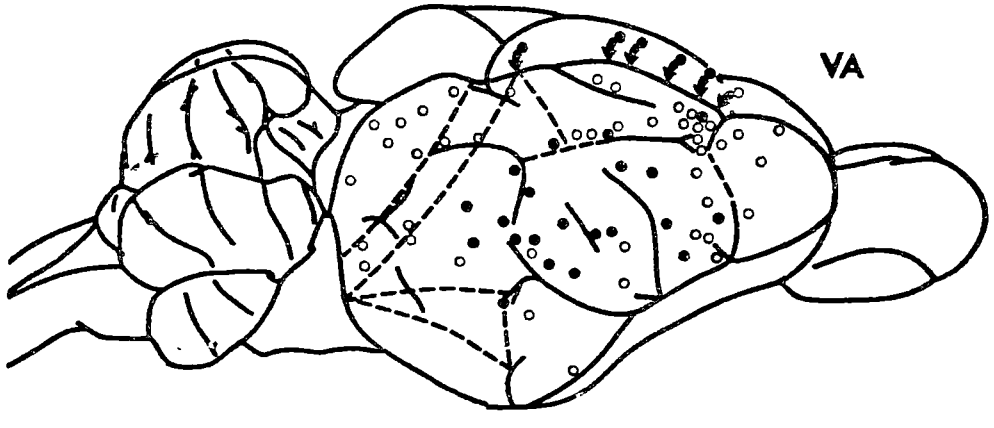


Figure 8

A. Cortical HRP injections in Trichosurus which produced retrograde labelling in the internal division of the ventrolateral nucleus (closed circles).

(For further details see Haight and Neylon 1979).



B. Cortical injections which labelled the ventroanterior nucleus.

is similar to Didelphis and differs from Trichosurus, in that the VA projection field corresponds largely to that for VL. Thus VA projects to rostral and medial parts only of the parietofrontal area. Caudal and rostral parts of the VA field appear to be preferentially related to lateral and medial parts of the nucleus respectively. This pattern is similar to that for VL and VP.

In his retrograde degeneration study Goldby (1943) concluded that VA in Trichosurus connects to much the same region as his ventrointermediate nucleus (= VL), that is, to medial and rostral parts of the parietofrontal area. The data he presented, however, do not preclude the possibility of more extensive projections.

Our Trichosurus material (Haight and Neylon 1977b, Haight et al 1980, 1983) shows not only that VA has very widespread cortical projections, but that these overlap the VLe field to only a limited extent. VA is related to the parietofrontal and posterior parietal areas (fig 8b). The total VA projection field is separated into two regions, with an apparently terminal free zone intervening. Significant, and in some cases rather intense retrograde labelling of VA cells, resulted from HRP injections into the extreme medial margin of the parietofrontal cortex (VPL/VLe

projection zones), the lateral parietofrontal cortex (VPM projection zone), and the posterior parietal area. Injections into the remainder of the VPL/VLe projection areas failed to produce detectable label in VA.

In general it was found that caudally placed injections preferentially labelled lateral parts of VA, while more rostrally placed injections labelled more medial parts of the nucleus. This ordering of thalamocortical connections parallels that for VP and VL, as in Dasyurus. No distinction was evident in the position of label in the nucleus following injections in the two parts of the VA field.

Finally, it must be noted that the rostral margin of the parietofrontal area in Trichosurus, and the rostromedial margin of this area in Dasyurus, receive connections from MD, as well as from VA and/or VL(e) (Haight and Neylon 1981b, Haight et al 1983).

Summary of Cortical Relationships and Comparison of Placental and Marsupial Organisation

In the cat and monkeys, and in the three marsupials examined so far, motor (or sensorimotor) cortex receives orderly projections from parts of the VA-VL complexes, with specific cortical loci related to

longitudinal cell columns in certain nuclei. The presently available data indicate that such an orderly organisation may not be present in the rat, and the prosimian Galago.

Various divisions of the VA-VL complexes in the cat and in monkeys have been shown to be connected to prefrontal and posterior parietal (cat and monkeys), and limbic (cat), as well as motor cortex, and there is some distinction between different nuclei in that VL (including VPLo or Vim in monkeys) projects mainly to motor cortex, while the other areas receive inputs mainly from VA.

The marsupial species can be compared in very general respects with the cat and monkeys, in that parts of the VA-VL complexes are related to (sensory) motor and posterior parietal cortex, and perhaps to a limited extent at least to the prefrontal area (as defined by the MD projection field).

In Didelphis VA and VL, which are difficult to separate on cytoarchitectural grounds, apparently have identical cortical projection fields. Projections from the VA-VL complex cover most of the parietofrontal area, extensively overlapping those from VP, except perhaps in the region of the second somatosensory area. Overlap extends even to the laminar distribution of

connections from the two regions of thalamus, although there are differences in terminal density. Trichosurus and Dasyurus, on the other hand, have restricted VLe or VL projection fields, which show a significant degree of separation from that for VP. The anatomical evidence for the varying degrees of convergence of these projections in the different marsupials is reflected by the findings of physiological studies.

Dasyurus resembles Didelphis in that VA connects to the same cortical region as VL, however in Trichosurus VLe and VA projections overlap only slightly. Some similarity is evident between Trichosurus and the cat and monkey, in that VA has more than one cortical target area, and in the relationship with the posterior parietal area. The Trichosurus VA, unlike that in the other animals, has only minor connections to prefrontal cortex, and to motor cortex (as delineated physiologically and by the extent of the VLe field). The extensive projections of VA to the lateral parietofrontal area, which contains the head sensory region and second somatosensory area, and which constitutes sensory, rather than sensorimotor or motor cortex (see below) has no parallel in any other species.

The small 'internal' division of VL, or VLi, in

Trichosurus projects discontinuously, and in a distinctive manner, to parts of the lateral parietofrontal cortex, and appears to be preferentially related to the barrel field. There is no obvious homologue for this nucleus in either Didelphis or Dasyurus, or in any placental animal examined to date.

(iii) FUNCTIONAL CONSIDERATIONS

SENSORY AND MOTOR CONVERGENCE IN THE VENTRAL TIER NUCLEI AND NEOCORTEX

Ventral Tier Nuclei

The general organisation of input connections from the principle somesthetic pathways and motor control centres to the ventral nuclear group is basically similar in all the mammals examined to date, in that these are largely or solely directed towards separate target areas.

In Didelphis, Trichosurus, and the rat, the spinal, dorsal column lemniscal and trigeminal projection fields appear to be essentially restricted to the VP complex (Didelphis, Mehler 1969, Walsh and Ebner 1973; Trichosurus, Rockel et al 1972; rat, Feldman and Kruger 1980, Lund and Webster 1967a,b, Smith 1973), while projections from the cerebellum, and in the case of the

rat at least, from the substantia nigra and pallidal complex, apparently terminate only in parts of VA-VL and/or VM (Didelphis, Martin et al 1974, Walsh and Ebner 1973; Trichosurus, Rockel et al 1972; rat, Beckstead et al 1979, Carter and Fibiger 1978, Donoghue et al 1979, Faull and Carman 1978, Haroian et al 1981).

In the cat and primates segregation is less complete, since in these animals some somesthetic pathway projections extend beyond the rostral boundaries of VP into restricted caudal parts of the VA-VL complexes (Asanuma et al 2983b, Berkley 1980, Jones and Burton 1974, Pearson and Haines 1980a, 1981, Tracey et al 1980). These regions appear to be, in part at least, specialised centres for the relaying of short latency deep receptor information to cortex (Asanuma et al 1979, Horne and Tracey 1979, Larsen and Asanuma 1979). The particular pathway(s) by which such information reaches these parts of the thalamus remains in some doubt (Tracey et al 1980). Apart from these specialised convergent zones, somesthetic and motor pathway terminal fields are segregated in the VP complex, and in the VA-VL complex and VM (or possible equivalent) respectively, as in the less advanced species (cat, Berkley 1980, Burton et al 1979, Hendry et al 1979, Jones and Burton 1974, Sugimoto et al 1981; primates, Asanuma et al 1983b, Boivie 1978, 1979,

Carpenter et al 1976, De Vito and Anderson 1982, Ganchrow 1980, Kalil 1981, Pearson and Haines 1980a, 1981 Tracey et al 1980). Within the VP complexes of these animals there is evidence for further functional separation, with different kinds of sensory information projecting preferentially to different regions of VPL (Berkley 1980, Boivie 1979, Jones and Friedman 1982, Loe et al 1977).

Somatosensory and Motor Cortex: Physiological Evidence

Mammals demonstrate varying degrees of overlap of somatic sensory and motor functions at the cortical level. This has been demonstrated by physiological methods in terms of the degree of overlap of those region(s) of cortex in which neurons respond most readily to stimulation of somesthetic receptors (somatosensory cortex), with those region(s) from which discrete body movements are elicited most easily by low intensity electrical stimulation (motor cortex).

The designation of specific cortical areas as 'somatosensory' or 'motor' implies only that these are their primary functions, since it is well known that somatosensory cortex is involved in movement control, and that motor cortex responds to somesthetic stimulation (see Woolsey 1958).

In certain mammals, including the monotremes, marsupials, edentates, hedgehog, rat and the prosimian Galago, somatosensory and motor cortex overlap significantly, though to varying extents. In the cat and more advanced primates the sensory and motor areas are completely separate (monotremes, Bohringer and

Rowe 1977, Lende 1964; marsupials, Abbie 1940, Adey and Kerr 1954, Golby 1939, Haight and Weller 1973, Lende 1963 a,b,c, Magalhaes-Castro and Saraiva 1971, Rees and Hore 1970, Weller and Haight 1973; edentates, Dom et al 1971, Royce et al 1975, Saraiva and Magalhaes-Castro 1975; hedgehog, Lende and Sadler 1967; rat, Hall and Lindholm 1974; prosimian (Galago), Kanagasuntheram et al 1966; cat and advanced primates, Woolsey 1958, 1964).

Lende (1969) has postulated, on the basis of physiological evidence from a variety of mammals, that a significant degree of sensory motor overlap in cortex is characteristic of a primitive level of organisation, and that the process of evolution of more advanced mammals has tended to produce an increasing separation of function. Numerous studies subsequent to his presentation of this theory (see references above) would appear to support this view, in fact in some advanced primates it is now evident that the primary somatosensory area contains several separate and functionally distinct body and head representations (Kaas et al 1979, Merzenich et al 1978, Nelson et al 1980).

Correlation between Physiological and Anatomical Evidence

The somatosensory and motor areas receive their major thalamic inputs from the VP and VA-VL complexes respectively. In those animals in which anatomical and physiological data can be compared there is for the most part a close correspondence between the degree of overlap of sensory and motor cortex, and the degree of convergence of ascending projections from VP and VA-VL.

Rat, Cat and Primates

In the prosimian Galago, sensory and motor cortex show considerable overlap (Kanagasuntheram et al 1966), as do VP and VL projections (Pearson and Haines 1980b).

In the rat there is a craniocaudal gradient of sensory motor overlap, with the head representations separate, the forelimb areas overlapping slightly, and the hindlimb areas overlapping completely (Hall and Lindholm 1974). Correspondingly, VP and VA-VL project separately to the sensory and motor head areas respectively, but are both connected to the combined hindlimb area (Donoghue et al 1979).

In the cat and advanced primates the physiological

evidence indicates that sensory and motor cortex are separate (Woolsey 1958, 1964). These animals, it will be remembered, show a degree of sensory motor convergence within the ventral tier nuclei, a factor which complicates comparison of cortical projections with other species which apparently lack such thalamic convergence. In both the cat and monkeys, however, it seems clear that those parts of the ventral tier which only receive inputs either from the major motor pathways (rostral VA-VL) or from somesthetic pathways (VP), project to separate areas of cortex, areas generally recognised as constituting motor and somatosensory cortex respectively (cat, Hendry et al 1979, Larsen and Asanuma 1979, Strick 1973; monkeys, Friedman and Jones 1981, Jones and Leavitt 1974, Jones et al 1979, Strick 1975, 1976a, Tracey et al 1980). Thus, in these animals too there is a certain consistency between anatomical and physiological findings. The convergent thalamic zones present special problems. In the cat this region, the 'spinal' part of VL, is probably connected to parts at least of sensory cortex, as well as to motor cortex (Larsen and Asanuma 1979, Spreafico et al 1981, Strick 1973). In monkeys, on the other hand, projections of the possible equivalent region (VPLo or Vim) are restricted to motor cortex (Friedman and Jones 1981, Jones et al 1979, Strick 1975, 1976a, Tracey et al 1980).

Monotremes, Edentates and Insectivores

Information on the degree of convergence of VP and VA-VL projections to cortex in monotremes, edentates, and insectivores such as the hedgehog is not presently available, however it seems reasonable to expect that this would parallel the varying, but in all cases significant, degree of overlap of the sensory and motor areas reported in physiological studies in these animals (Bohringer and Rowe 1977, Lende 1964, Lende and Sadler 1967, Royce et al 1975, Saraiva and Magalhaes-Castro 1975).

Marsupials

In marsupials the picture with respect to the extent of sensory motor overlap in the cortex seems quite clear cut in Didelphis and Dasyurus but somewhat more complex in Trichosurus and in wallabies.

The electrophysiological mapping studies of Lende (1963a,b) and Magalhaes-Castro and Saraiva (1971), showed that in two species of American opossums there is a complete overlap of motor and primary sensory cortex. In one of these, the Virginia opossum Didelphis virginiana, the VP and VA-VL cortical projection fields overlap to a corresponding degree

(Donoghue and Ebner 1981a, Killackey and Ebner 1973).

In Dasyurus the cortical projections of VP and of VL and VA overlap extensively but not completely (Haight and Neylon 1981b). Sensory cortex has not been mapped using physiological methods in this animal, and, as stated previously, the VA-VL projection fields do not correspond exactly to the location of the motor cortex delineated by Abbie's (1940) stimulation study. Nevertheless, his results clearly indicate that motor cortex is restricted in extent, and is located in rostral and medial parts of the parietofrontal area. Thus in general terms the available anatomical and physiological data correspond. The anatomical results in particular provide strong evidence for a degree of separation of sensory and motor cortex in this animal.

The results of electrophysiological mapping studies of sensory (Adey and Kerr 1954, Haight and Weller 1973 plus unpublished observations) and motor cortex (Abbie 1940, Goldby 1939, Rees and Hore 1970), together with our anatomical findings with respect to the distributions of the cortical projections of VP and the external division of VL(VLe) (Haight and Neylon 1978b, 1979), indicate a significant degree of separation of sensory and motor cortex in Trichosurus, similar to that suggested by the Dasyurus data.

Some problems do arise with respect to the distribution of cortical projections from other parts of the VA-VL complex in Trichosurus. While most of the lateral parietofrontal cortex, or head sensory representation area and second somatosensory cortex, lacks VLe connections, some parts do receive inputs from the internal division of VL (VLi), and from VA.

No definitive function can yet be assigned to VLi since nothing is known of its input connections. Its position in the ventral nuclei complex would suggest that, as with the neighbouring members of the VA-VL complex, this small region has some role in movement control systems. The nucleus projects discontinuously, and in a distinctive manner, to lateral parietofrontal cortex (fig 8a), and appears to be preferentially related to the barrel field (Weller 1972). On the basis of this relationship we have suggested that VLi is a specialised centre, peculiar to Trichosurus and perhaps to other marsupials which possess cortical barrels, which may be involved in relaying proprioceptive information to the cortex from vibrissae (Haight and Neylon 1979). Whatever proves to be the case VLi and its input and output connections would appear to be a system distinct from, and additional to, the main pathways by which 'motor' information reaches the cortex, with no obvious homologue in any other species examined to date. The presence of VLi

projections to lateral parietofrontal cortex then need not be considered as contradictory to the evidence outlined above for a significant degree of separation of the regions with primarily sensory and motor functions.

The sources of afferent connections to VA in Trichosurus and other marsupials are not known. The nucleus apparently does not receive cerebellar connections, although it seems reasonable to expect inputs from some other major motor control centres, such as the entopeduncular nucleus and/or substantia nigra. In lacking cerebellar connections, however, VA would clearly be involved in relaying different kinds of 'motor' information to cortex to that provided by the massive cerebellothalamocortical system, involving VL(e) in Trichosurus, and various parts of the VA-VL complex in other animals, which constitutes the principle or definitive subcortical input to the (electrophysiologically delineated) motor cortex.

Thus, VA projections to those parts of the lateral parieotofrontal cortex in Trichosurus (fig 8b) which lack VLe (cerebellothalamocortical system) inputs, and in which low intensity electrical stimulation fails to produce discrete body movements, may be considered as providing some form of direct input from the 'motor'

thalamus to regions of cortex which must still be regarded as having primarily a sensory function. An analagous situation occurs with the projections reported from the 'spinal' zone of the cat VL to areas of cortex considered to be primarily somatosensory in function (Larsen and Asanuma 1979, Spreafico et al 1981, Strick 1973).

From Abbie's (1940) electrical stimulation studies in two species of wallaby (Macropus ruficollis and Macropus agilis), and later microelectrode mapping studies in the Tasmanian pademelon or rufous wallaby Thylogale billardierii (Weller et al 1977), a picture emerges of a degree of sensory and motor cortex overlap in this group of animals very similar to that seen in Trichosurus (and also Dasyurus), as might be expected in such closely related species. On the other hand, Lende (1963c) reported that in Thylogale (= Macropus) eugenii the motor and primary somatosensory areas showed the same degree of overlap as that seen in Didelphis. This fundamental disagreement between the two sets of available data obviously requires resolution.

SOMATOTOPIC ORGANISATION WITHIN THE SOMATOSENSORY AND MOTOR CORTEX

In addition to varying degrees of functional overlap, different mammals also exhibit variations in the internal organisation of the principal motor, and to a lesser extent somatic sensory cortical areas.

Primary Somatosensory Cortex

Somesthetic information from different parts of the body and head reaches the primary sensory cortex via VP in an orderly, somatotopically organised pattern. This pattern in most mammals can be crudely represented in the form of an inverted figurine, with the limbs directed rostrally. Such an arrangement has been described in monotremes (Bohringer and Rowe 1977, Lende 1964), marsupials (Adey and Kerr 1954, Haight and Weller 1973 plus unpublished observations, Johnson et al 1973, Lende 1963a,c, Megalhaes-Castro and Saraiva 1971, Pubols et al 1976, Weller and Haight 1973, Weller et al 1976, 1977), and numerous placental species (Hall and Lindholm 1974, Lende and Sadler 1967, Royce et al 1975, Saraiva and Megalhaes-Castro 1975, Welker 1971, Woolsey 1958, 1964). The organisation in advanced primates, however, is now known to be more complex, with the primary sensory area containing multiple body and

head representations, each receiving information from particular receptor populations (Kaas et al 1978, Merzenich et al 1978, Nelson et al 1980).

Motor Cortex

The organisation of motor cortex shows a far greater degree of variability in different groups of mammals. With the exception of the edentates the primary motor area in placental species is generally considered to have a somatotopic arrangement which is a mirror image to that in the primary somatosensory area (Hall and Lindholme 1974, Lende and Sadler 1967, Woolsey 1958, 1964). In some advanced primates this general organisation is complicated by the presence of multiple representations of some body parts (Strick and Preston 1978a,b, 1982a,b).

The edentate placentals follow the organisation found in Didelphid marsupials, with the overlapping (though incompletely so in the armadillo) sensory and motor areas having the same orientation (marsupials, Lende 1963a,b, Magalhaes-Castro and Saraiva 1971; armadillo, Royce et al 1975; sloth, Saraiva and Magalhaes-Castro 1975).

Among the monotremes, the echidna may show elements of both of these arrangements, in possessing a caudal

motor region with similar orientation to the somatosensory area, which it overlaps, and a second rostral motor representation with uncertain orientation (Lende 1964).

This leaves the question of orientation in the motor cortex of Australian marsupials. According to Lende (1963c) the body representation in motor cortex of the wallaby Thylogale (= Macropus) eugenii shows the same orientation as, and fully overlaps, that in the primary somatosensory area. This suggests that Australian marsupials are organised along the same lines as Didelphis. The discrepancy between Lende's and others results with respect to the degree of overlap of motor and somatosensory cortex has already been discussed, and with this matter in some doubt, there must also be some question as to orientation of the motor representation. Unfortunately other studies of motor cortex in Australian marsupials provide insufficient detail to clearly determine anything other than orientation with respect to rostral and caudal body parts (Abbie 1940, Goldby 1939, Rees and Hore 1970). The study by Rees and Hore (1970) in Trichosurus does provide a hint (see their fig 1) that in this species at least the motor area may have a reversed somatotopic organisation. If this were the case the motor cortex in Trichosurus, and possibly other Australian marsupials, would be more comparable

to that of the rat, both in terms of orientation and degree of overlap with somatosensory cortex (Hall and Lindholm 1974), than to that of Didelphis. This would represent a remarkable degree of divergence between the Australian and American groups.

In the absence of more definitive information, however, Lende's (1963c) evidence for a parallel somatotopic organisation in the primary sensory and motor areas in the wallaby must stand for the present. Trichosurus and other related Australian marsupials are presumably organised along similar lines to the wallaby. In terms of the somatotopic organisation and degree of overlap of sensory and motor cortex, then, Australian marsupials may be comparable to the edentate placental species, the armadillo, since electrophysiological mapping of the cortex in this animal has shown parallel but slightly separated primary somatosensory and motor representations (Royce et al 1975).

SUMMARY AND CONCLUSIONS

Mammals show varying degrees of overlap of those regions of cortex shown by electrophysiological methods to have primarily a somatosensory or motor function, with a tendency towards increasing separation in more 'advanced' forms. With the exception of small

specialised zones where convergence occurs in the cat and primates, somesthetic and 'motor' pathways inputs are segregated within the ventral tier nuclei. The degree of functional overlap in the cortex of different animals is reflected by the degree of convergence of ascending projections from these separate somesthetic and 'motor' (cerebellar projection zone) regions. Dasyurus and Trichosurus, representing the two main groups of Australian marsupials, demonstrate a significant degree of separation of sensory and motor cortex, indicating that these animals have diverged considerably from the presumed stem marsupial condition, as represented by Didelphis. If one accepts that the total sensorymotor overlap seen in Didelphis (Lende 1963a, b, Magalhaes-Castro and Saraiva 1971) and some edentates (Saraiva and Magalhaes-Castro 1975) represents a primitive level of organisation, then Trichosurus and Dasyurus may be considered to show convergent development of the more advanced pattern evident in most placental species, and to be in particular comparable to the rat (Hall and Lindholm 1974). The question of the degree of functional overlap in the cortex of wallabies is as yet unresolved, since the presently available evidence is conflicting. Some findings indicate a Didelphis type of organisation, and others suggest similarities to the Trichosurus and Dasyurus arrangement. The latter situation would seem more likely since the Australian

species are in other respects more closely related to each other than to Didelphis (Kirsch 1977).

Apart from variable overlap, the somatotopic organisation of the main motor, and to a lesser extent somatosensory cortical areas, varies considerably in different groups, primarily in terms of the orientation of the motor representations. The question is raised as to whether Australian species necessarily follow the Didelphis (and edentate) organisation of parallel orientations of the motor and somatosensory representations, or whether divergence has occurred in this respect as well as in the degree of functional overlap.

(d) VENTROMEDIAL NUCLEUS

(i) SUBCORTICAL AFFERENT CONNECTIONS

Placentals

The inputs to VM in placental species which best differentiate this region from other parts of the ventral group are probably those from the substantia nigra (SN). Heavy projections, originating primarily or solely in the pars reticulata, the non dopaminergic sector of the SN, have been demonstrated in the rat

(Beckstead et al 1979, Clavier et al 1976, Herkenham 1979) and cat (Glenn et al 1982, Hendry et al 1979, Kultas- Ilinsky et al 1978, Rinvik 1975).

It is not clear which, if any, region in monkeys is exactly homologous to VM of other species. As stated previously Walker (1938) and Olszweski (1952) did not recognise a VM in their descriptions of the rhesus monkey thalamus, and most subsequent authors have applied their systems of thalamic subdivisions and nomenclature in studies of primate thalamic connections. Possible equivalents are found in the regions usually designated as the medial division of VL (VLm), and also perhaps the magnocellular division of VA (VAmc), since these receive strong nigral projections in the rhesus monkey (Carpenter et al 1976).

Major cerebellar connections to VM are present in the rat (Donoghue et al 1979, Faull and Carman 1978, Haroian et al 1981, Herkenham 1979), and the weight of evidence indicates that the same is true of the cat (Angout and Bowsher 1970, Kievit and Kuypers 1972, Kultas- Ilinsky et al 1980, Sugimoto et al 1981, but see Hendry et al 1979). In monkeys, however, there would appear to be no equivalent pathways (Batton et al 1977, Kalil 1981, Kievit and Kuypers 1972, Miller and Strominger 1977).

Projections from the entopeduncular nucleus to lateral VM, and from the medial pallidal segment to lateral VLm, but not VAmc, have been demonstrated in the rat and cat, and in the rhesus monkey respectively. Some direct projections to these centres also appear to be present from the external pallidal segment in the rat and monkey (rat, Carter and Fibiger 1978, Herkenham 1979, Severin et al 1976; cat, Glenn et al 1982, Hendry et al 1979, and see also Larsen and McBride 1979, Nauta 1979; monkeys, De Vito and Anderson 1982, Kim et al 1976, Kuo and Carpenter 1973, Nauta and Mehler 1966).

Finally, there is also evidence for projections from the deeper layers of the superior colliculus to VM in the rat and cat (Glenn et al 1982, Herkenham 1979), and VLm in the monkey (Harting et al 1980), and from the central grey, parabrachial nucleus, and medullary reticular centres to VM in the rat (Herkenham 1979) and cat (Glenn et al 1982).

Marsupials

The output connections of the substantia nigra and entopeduncular nucleus have unfortunately not yet been examined in any marsupial species, and only limited information is available on subcortical afferents to

VM.

Although they examined cerebellothalamic projections, Rockel et al (1972) did not describe any connections with VM in Trichosurus, however a cerebellar input to the region has been reported in Didelphis (Martin et al 1974). In the Trichosurus study by Rockel's group, one experimental animal (experiment 16 fig 7) displayed extensive, though rather light, terminal degeneration in VM following a contralateral medullary lesion which was centred on the dorsal column nuclei, but which also involved several other regions, including the solitary, spinal trigeminal and vestibular nuclei, and the lateral tegmental area. They interpreted this result as signifying a gustatory projection, in light of the damage to the solitary nucleus. As discussed previously, however, the existence of direct contralateral solitariothalamic projections in mammals is in some doubt. Also, it would seem unlikely that gustatory projections would have such an extensive terminal field, since in many other species the thalamic gustatory centre is a small and rather well defined cell group (see VPMpc discussion for references). In light of the involvement of a number of other centres by their lesion the significance of their findings must remain in doubt. One possibility is that the degenerating fibres originate in part or parts of the medullary tegmental

fields, since connections to VM from such regions have been described in the rat (Herkenham 1979) and cat (Glenn et al 1982).

Summary of Subcortical Afferent Connections and Comparison of Placental and Marsupial Organisation

VM in the rat and cat receives both nigral and cerebellar inputs, as well as connections from the entopeduncular nucleus to its lateral margin. In monkeys the regions designated VLm and VAmc may be equivalent to VM in the other species in light of the presence of nigral projections to these centres. In addition, the medial pallidal segment projects to the lateral margin of VLm (though not to VAmc). Direct projections from the external pallidal segment to the rat VM, and monkey VLm have also been reported. On the other hand, however, neither VLm nor VAmc in monkeys receive cerebellar connections. Thus these centres cannot be considered to be completely homologous to the rat and cat VM.

In the rat and cat VM also has been shown to receive projections from a variety of brainstem centres.

In the marsupials Didelphis differs from Trichosurus in that cerebellar projections to VM have been reported

only in the former species. Didelphis is therefore comparable to the rat and cat in this respect. There may be some basis for comparison of the Trichosurus VM with that of the rat and cat in regard to possible connections from the medullary tegmental fields.

(ii) CORTICAL RELATIONSHIPS

Placentals

The rat and cat VM and rhesus monkey VLm (and VAmc), have been shown to project heavily to prefrontal cortex, and to the rostral part at least of the motor areas (rat, Herkenham 1979, Jones and Leavitt 1974; cat, Glenn et al 1982, Niimi et al 1977, 1981a; monkey, Kievit and Kuypers 1977). Descending projections from these areas to the nucleus are present in the rat (Herkenham 1979) and cat (Glenn et al 1982, Rinvik 1968b,c).

Herkenham (1979) found that the rat VM, though projecting primarily to rostral cortical areas, also had diffuse connections throughout most of the remainder of the cortex. A similar widespread distribution of cortical connections from the nucleus has been reported in an early degeneration study in the cat (Smaha and Kaelber 1967), and more recently in the

tree shrew (Divac and Passingham 1980). In the case of the cat, however, a recent study by Glenn et al (1982), using anterograde and retrograde tracing and electrophysiological techniques, found no evidence for VM connections outside the rostral motor and prefrontal areas.

Marsupials

The cortical relationships of VM in the marsupials examined to date show certain general similarities. In Trichosurus and Dasyurus the nucleus projects heavily, and in an orderly manner, to the rostral margin of the parietofrontal area (fig 9), and also to the caudal part at least of the prefrontal area, as defined by the MD projection field (Haight and Neylon 1981b, Haight et al 1983 , Neylon and Haight 1977). Donoghue and Ebner (1981a) described widespread VM projections to the parietofrontal area in Didelphis. VM projections also overlapped part at least of the prefrontal area (MD field) in the 'postorbital' cortex. No particular organisation pattern was found for these projections in Didelphis. In Trichosurus and Didelphis the VM-cortical relationships appear to be reciprocal (Donoghue and Ebner 1981a, Haight et al 1983, Rockel et al 1972).

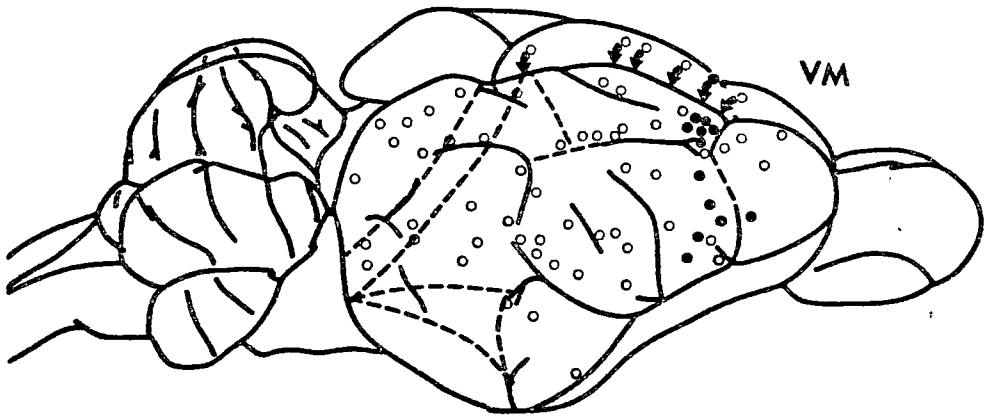


Figure 9

Cortical HRP injections in Trichosurus which produced retrograde labelling of the ventromedial nucleus (closed circles).

Summary of Cortical Relationships and Comparison of Placental and Marsupial Organisation

Some general parallels can be drawn between marsupial and placental organisations with respect to the cortical relationships of VM. In placental animals the nucleus (or possible equivalent) is primarily related to prefrontal cortex and at least the rostral margin of the motor area, although in some animals more widespread connections appear to be present.

The full extent of VM connections with prefrontal cortex in the marsupials is not known, however the nucleus is related to at least the caudal margin of this area. In the Australian species the VM projection field in the parietofrontal area corresponds in large part to the rostral margin of the motor cortex, as defined both by electrophysiological studies (Abbie 1940, Goldby 1939, Rees and Hore 1970) and by the VLe/VL projection fields (Haight and Neylon 1979, 1981b), although there is also some encroachment onto rostral lateral sensory (head representation) cortex (Haight and Neylon 1981b, Haight et al 1983, Neylon and Haight 1977). In Didelphis VM projections are more widespread, though it must be remembered that in this animal the motor cortex extends over most of the parietofrontal area (Donoghue and Ebner 1981a, Lende

1963b). The marsupials can be said then to conform generally to the placental organisation in that VM is primarily related to the motor and prefrontal areas.

(iii) FUNCTIONAL CONSIDERATIONS

The functional role(s) of VM remain unclear. The presence of inputs from the substantia nigra, pallidum and in some cases at least, cerebellum, suggest motor functions, which are in keeping with its relationship with motor cortex. Projections from a variety of other subcortical centres, as well as those to prefrontal cortex and possibly to other cortical areas in some species, however, indicate that the region probably has other roles. Its cortical projections are not restricted to specific functional areas, but are distinct from most other thalamic centres in being primarily directed to lamina 1 (Divac and Passingham 1980, Glenn et al 1982, Herkenham 1979), which supports the view that VM may be responsible for so called 'recruiting responses', at least in rostral parts of the cortex (Glenn et al 1982 and Herkenham 1979 for discussion).

(e) SUBMEDIUS NUCLEUS

(i) SUBCORTICAL AFFERENT CONNECTIONS

The only afferent connections of SM known at present for any species are those demonstrated by Craig and Burton (1981) from the spinal cord and caudal trigeminal nucleus in the rat, cat and monkey.

(ii) CORTICAL RELATIONSHIPS

In the rat and cat accounts vary as to the exact or heaviest distribution of SM connections to cortex, however they would seem to be spread over a large part of the prefrontal area in each case, on both the medial and lateral surfaces of the hemisphere (rat, Jones and Leavitt 1974, Krettek and Price 1977a; cat, Craig et al 1982, Niimi et al 1977, 1981a). In the cat the nucleus receives reciprocal connections from these cortical areas (Craig et al 1982). Also in the cat, projections from SM to limbic cortex have been described (Niimi et al 1978).

Bodian (1943) found that SM (his VM) in Didelphis underwent severe retrograde degeneration following lesions which involved the 'pre and postorbital' areas, which lie immediately rostral to the parietofrontal area on the lateral surface of the hemisphere. Similarly, HRP injections into the 'postorbital' area in Donoghue and Ebner's (1981a) study produced substantial retrograde labelling in what would appear

to be SM (their rostral VM). Bodian considered that the SM projection field was largely separate from that of MD, however in Donoghue and Ebner's material MD was also labelled by injections in the 'postorbital' area. If one accepts Rose and Woolsey's (1948) definition of the prefrontal area as that area of cortex receiving MD projections, (see Medial Nuclei), then SM is related to part at least of the prefrontal area in this animal.

We obtained no information on the connection of SM in our Dasyurus study (Haight and Neylon 1981b), which examined only the parietofrontal area. Injection of HRP into the rostral margin of this area produced extensive and intense retrograde labelling of cells in several centres adjacent to, and in fact surrounding SM, but spared this nucleus. The question of which, if any, cortical region in Dasyurus receives SM connections, must therefore remain open, although it seems reasonable to expect a similar arrangement to that found in other species.

(iii) FUNCTIONAL CONSIDERATIONS

The nucleus, in placental species at least, appears to be primarily concerned with the transmission of nociceptive information (Craig and Burton 1981, Craig et al 1982), and its connections with areas of cortex

related to 'limbic' functions would suggest a role in the 'emotional' or 'motivational' aspects of pain responses (Melzack and Casey 1968).

LATERAL NUCLEI

1. DESCRIPTIONS AND COMPARISONS OF NUCLEAR STRUCTURE IN MARSUPIALS

(For illustrations see Haight and Neylon 1978a figs 4-11, Haight and Neylon 1981a figs 4-12, Oswaldo-Cruz and Rocha-Miranda 1967 figs 5-13).

This group is divided into lateroanterior (LA), laterointermediate (LI), and lateroposterior (LP) nuclei. Some important differences in the internal structure of LI and LP are evident between *Didelphis* on the one hand, and *Trichosurus* and *Dasyurus* on the other.

The nomenclature presently applied to the members of this group corresponds to that used by Bodian (1939) and Oswaldo-Cruz and Rocha-Miranda (1967) in their descriptions of the *Didelphis* thalamus. We have modified Goldby's (1941) original treatment of the lateral group in *Trichosurus*. His 'lateralis B' nucleus, later considered as the 'lateralis B' component of the posterior nuclear complex (Pob) in this animal by Rockel et al (1972), is now simply the main rostral part of the posterior nucleus (PO) (Neylon

and Haight 1983). Goldby noted, but did not give separate status to, a small lateral portion of his 'lateralis A' nucleus. We have recognised this region as a distinct nucleus in both Trichosurus and Dasyurus. Otherwise Goldby's 'lateralis A' nucleus corresponds to our laterointermediate nucleus (Haight and Neylon 1978a, 1981a).

LI in the three marsupials first appears rostrally at the dorsal aspect of the anteroventral nucleus, which it replaces at more caudal levels. This large nucleus then occupies much of the cross sectional area of the dorsal surface of the thalamus, until it is in turn replaced by PO and LP. The border between LI and LP is easily recognised, while that between LI and PO is indistinct.

LA is a small but fairly distinct cell group adjoining the lateral boundary of LI in the three animals. The two nuclei have similar cytoarchitecture, but are consistently separated by a thin cellfree lamina.

In Trichosurus and Didelphis LP is approximately co-extensive with the dorsal lateral geniculate nucleus (LGd), which it borders medially. In Dasyurus the LGd extends some distance rostral to LP.

LI is clearly divisible into dorsal and ventral parts in Didelphis, but appears to be homogeneous in Trichosurus and Dasyurus. On the other hand, LP shows distinct medial and lateral divisions in the two Australian species, but not in Didelphis (Haight and Neylon 1978a, 1981a, Oswaldo-Cruz and Rocha-Miranda 1967).

2. CONNECTIONS AND FUNCTIONS OF THE LATERAL NUCLEI

Nothing is known of the afferent and efferent connections of LA in marsupials, and at present this centre has no obvious homologue in any placental species. Comparisons can, however, be made between the marsupial LI and LP and similarly located regions in placentals.

(a) LATEROINTERMEDIATE NUCLEUS

(i) SUBCORTICAL AFFERENT CONNECTIONS

The marsupial LI would appear to be comparable, in terms of position and main afferent connection, to the division of the lateral complex of placental animals usually referred to as the laterodorsal nucleus (LD).

The principle afferent connections of LD would appear to arise from the pretectal complex (tree shrew, Weber

and Harting 1980; rat, Robertson et al 1979, 1980a, Ryszka and Heger 1979; cat, Berman 1977, Itoh 1977, Robertson et al 1980b). Additional inputs have also been reported from the zona incerta, dorsolateral tegmental nucleus and lateral hypothalamus in the rat (Ryszka and Heger 1979).

No information is available on the input connections of LI in Trichosurus or Dasyurus, however a pretectal projection has been reported in Didelphis (Benevento and Ebner 1970).

(ii) CORTICAL RELATIONSHIPS

Placentals

Numerous studies in placental species have shown that LD is strongly and reciprocally related to the limbic cortex on the dorsomedial surface of the hemisphere, and to the parahippocampal region (rat, Beckstead 1976, Jones and Leavitt 1974, Robertson and Kaitz 1977, Robertson et al 1979, 1980a, Segal 1977, Spiro et al 1980; cat, Kaitz and Robertson 1980, Niimi and Inoshita 1971, Niimi et al 1978, Robertson and Kaitz 1981; monkeys, Locke and Kerr 1973, Powell 1973, Yakovlev et al 1960, 1966). There is some disagreement over possible projections to the posterior parietal and

peristriate regions, these having been reported by some authors (rat, Coleman and Clerici 1980, McDaniel et al 1978; cat, Berson and Graybiel 1978, Niimi and Inoshita 1971, Niimi et al 1979; monkey, Kasdon and Jacobson 1978), but not others (rat, Jones and Leavitt 1974, Spiro et al 1980; cat, Tanji et al 1978; monkey, Divac et al 1977). Robertson (1977), and Robertson and Kaitz (1977) reported sparse LD projections to posterior parietal cortex in the cat, but later (Robertson and Kaitz 1981) suggested that these may arise from parts of the pulvinar which had been incorrectly placed with LD. The weight of evidence would suggest, however, that LD probably is connected to this region of cortex, although such connections may be rather sparse in comparison to those to the limbic cortex.

Marsupials

No definitive information is available on the thalamic relationships of limbic cortex in marsupials, and so it is not possible to state whether LI projects to these regions. The nucleus is, however, reciprocally connected to the posterior parietal area in Trichosurus (Goldby 1943, Haight et al 1980 and see fig 10). Projections from LI to this region have also been reported in Didelphis (Coleman and Clerici 1981, Coleman et al 1977, Donogue and Ebner 1981a). In our

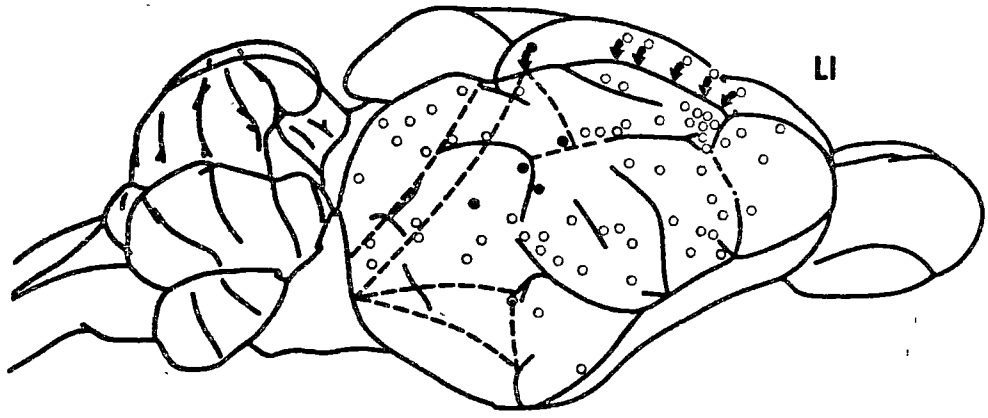


Figure 10

Cortical HRP injections in Trichosurus which produced retrograde labelling in the laterointermediate nucleus (closed circles).

Trichosurus material HRP injections in this region produced only very faint labelling of LI cells compared to that seen in other thalamic nuclei, which would suggest that the major projections of the nucleus are directed elsewhere, possibly to limbic cortex.

(iii) FUNCTIONAL CONSIDERATIONS

Little can be said about the functions of LD (and LI?), apart from a general comment that the nucleus is clearly involved in limbic system circuitry. Robertson et al (1980a) have suggested that LD may relay visual and somesthetic information from the pretectum to limbic cortex.

(b) LATEROPOSTERIOR (PULVINAR) NUCLEI

The regions variously referred to as the lateroposterior nucleus or complex (LP), pulvinar nucleus or complex, or LP-pulvinar complex in different mammals, are broadly comparable in terms of their locations within the thalamus, and of their major afferent and efferent connections. Significant interspecies differences are evident, however, in their cytoarchitectural subdivisions, and in the distribution of certain of their afferent and efferent projections. This situation often makes the identification of possible homologous zones in different animals

difficult or impossible. An additional complication is added by the use of varying systems of nuclear parcellation and nomenclature in certain species, in particular the cat (e.g. compare Berson and Graybiel 1978, Niimi et al 1981b, Updyke 1977, and see Hughes 1980, Updyke 1981 for discussions of this problem).

(i) SUBCORTICAL AFFERENT CONNECTIONS

Placentals

It is widely accepted that in placental animals the main subcortical input connections to the LP-Pulvinar complex originate in the superior colliculus, and more specifically in the superficial collicular laminae, which in turn receive direct retinal and visual cortical projections. In most though not all species, the tectal pathways terminate primarily or exclusively in restricted portions of the LP-Pulvinar complex. The location and extent of these 'tectorecipient' zones vary in different animals, although common organisational plans are apparent within the rodent and primate orders. Members of each of these groups also exhibit similar cytoarchitectural subdivisions within the LP-pulvinar complexes (hedgehog, Hall and Ebner 1970; tree shrew, Albano et al 1979, Harting et al 1973a; rat, Perry 1980; hamster, Crain and Hall 1980;

squirrel, Robson and Hall 1977; cat, Berson and Graybiel 1978, Graham 1977; prosimian (Galago), Glendenning et al 1975, Racszkowski and Diamond 1980; monkeys, Benevento and Fallon 1975, Harting et al 1980, Mathers 1971, Partlow et al 1977, Trojanowski and Jacobson 1975b).

Lesser inputs from the retina, pretectum and cerebellum to restricted regions lateral to, and separate from, the tectal zone have been reported in the cat (Berman 1977, Berson and Graybiel 1978, Itoh 1977, Itoh et al 1979), and small and variably located, though still separate from the tectal field, retinal terminal areas described in the hamster (Crain and Hall 1980) and some advanced primates (Campos-Ortega et al 1970a). A possible retinal input to LP has also been reported in an Australian rodent, Rattus villosissimus (Mayner et al 1980).

In addition to these connections, retrograde labelling studies involving HRP injections in the monkey pulvinar (Trojanowski and Jacobson 1975b) and the cat LP (Rodrigo-Angulo and Reinoso-Suarez 1982) provide evidence for a number of other afferent projections. In the monkey retrogradely labelled cells were found in the claustrum, thalamic reticular nucleus, and dorsal lateral geniculate nucleus, while in the cat numerous brainstem centres were labelled, including the locus

coeruleus, parabrachial nuclei, dorsal tegmental nucleus, periaqueductal gray, mesencephalic reticular formation, raphe nuclei and the oculomotor nuclei. These brainstem centres in the cat apparently project primarily to the non 'tectorecipient' parts of LP, although their precise terminal fields remain to be determined. The visual cortex appears to be a major source of input connection to some at least of the 'non tectal' parts of the LP-Pulvinar complex in many species (see below).

Marsupials

The lateroposterior nuclei of Didelphis and Trichosurus have been shown to receive massive projections from the superior colliculus. The specific origins of these tectal projections are not known, however it seems likely that, as in placental species, they arise from the superficial laminae. In Didelphis tectal fibres apparently terminate throughout LP, which is cytoarchitecturally homogeneous, whereas in Trichosurus they are almost entirely restricted to the structurally distinct medial division of the nucleus (Benevento and Ebner 1970, Martin 1969, Rafols and Matzke 1970, Rockel et al 1972).

Benevento and Ebner (1970) reported a minor pretectal

projection to LP in Didelphis, which, unlike that in the cat, is relatively diffuse and not segregated from the tectal field. A small region in the dorsal part of LP has been shown to receive direct retinal projections in two species of American opossum (Royce et al 1976), and in Trichosurus and numerous other Australian marsupials (Pearson et al 1976, Rockel et al 1972, Sanderson and Pearson 1977, 1981, Sanderson et al 1978, 1979, 1983). This retinal input zone would appear to be similarly located to that in the hamster (Crain and Hall 1980), but not to those in the cat (Berson and Graybiel 1978, Itoh et al 1979), or primates (Campos-Ortega et al 1970a). In Trichosurus, and probably also in Didelphis, the region in question, unlike those in any of the placental species, lies within the tectal projection field (Benevento and Ebner 1970, Rockel et al 1972).

Summary of Subcortical Afferent Connections and Comparison of Placental and Marsupial Organisation

The marsupial LP receives subcortical input projections from the same major sources as the placental LP-Pulvinar complexes. The pattern of retinal connections to LP would appear to be common to all marsupials, and is similar to that in at least one rodent, but not the cat and primates. Didelphis and Trichosurus differ markedly in the extent of tectal inputs to LP, apparently reflecting the differences between them in

the cellular organisation of the nuclei. Considerable interspecies variability is also evident in the organisation of tectal projections to the placental LP-pulvinar complex, although common plans are evident within the rodent and primate orders.

Interestingly, despite this great variability in tectal projections in different mammals, and even between such related forms such as Trichosurus and Didelphis, some parallels can be drawn between Trichosurus and the cat. In both animals medial parts of the LP-Pulvinar group are the main or sole recipients of tectal fibres (Berson and Graybiel 1978, Rockel et al 1972).

(ii) CORTICAL RELATIONSHIPS

The detailed organisation of connections between the LP-Pulvinar complex and cortex also varies considerably between species, and even between members of particular mammalian orders (e.g. see Racszkowski and Diamond 1980 for discussion of variations in primates). In very general terms, however, the cortical relationship of the LP-pulvinar region are similar in most animals.

Placentals

The LP-Pulvinar group has been shown to have extensive

and heavy projections to regions of extrastriate cortex adjoining the striate or primary visual area in all placental species examined so far. Recent studies in some animals have extended the total projection field of the complex to include regions of temporal cortex adjacent to the major visual areas, and the posterior parietal cortex. In addition, in most though not all species, significant projections have been reported to the striate area. These vary greatly in density, but are particularly heavy in the cat and primates. In those animals for which information on descending cortical connections is available, it is clear that the thalamocortical relationships are generally reciprocal, although in some cases (e.g. squirrel, cat) parts of the nuclear complex receive inputs from cortical regions different from,or additional to,those to which they project (hedgehog, Gould et al 1978; tree shrew, Harting et al 1972, 1973b; rat, Hughes 1977, Jones and Leavitt 1974, McDaniel et al 1978, Olavarria 1979, Perry 1980; hamster, Crain and Hall 1980, Dursteler et al 1979; squirrel, Kaas et al 1972b, Robson and Hall 1977; rabbit, Karamanlidis and Giolli 1977; sheep, Karamanlidis et al 1979; cat, Berson and Graybiel 1978, Hughes 1980, Itoh et al 1979, Miller et al 1980, Mizuno et al 1975, Niimi et al 1979, 1981b, Robertson 1977, prosimian (Galago), Carey et al 1979, Glendenning et al 1975, Racszkowski and Diamond 1980; lemur, Cooper et al 1979; monkeys, Benevento and Davis 1977, Benevento and

Rezak 1976, Divac et al 1977, Graham 1982, Graham et al 1979, Kasdon and Jacobson 1978, Ogren 1977, Ogren and Hendrickson 1976, 1977, Rezak and Benevento 1979, Trojanowski and Jacobson 1975a, Wong-Riley 1977).

Marsupials

In Didelphis and Trichosurus the lateroposterior nuclei project to both striate and peristriate visual cortex, and to the posterior parietal area, and in turn receive descending projections from these regions (Didelphis, Benevento and Ebner 1970, Coleman and Clerici 1981, Coleman et al 1977, Martin 1968, Martin et al 1975; Trichosurus, Haight et al 1980, Rockel et al 1972). Thus, the marsupial organisation is basically similar to that of many placental species. In Didelphis the lateral part of LP is preferentially related to the striate and immediate peristriate cortex, and caudomedial LP to the posterior parietal area (Benevento and Ebner 1970, Coleman and Clerici 1981). A somewhat different arrangement is seen in Trichosurus, where the lateral and medial divisions of LP project mainly, though not exclusively, to the striate and peristriate areas respectively, and both divisions project to the posterior parietal area (Haight et al 1980 and see fig 11). Some degree of similarity between Trichosurus and Didelphis is evident

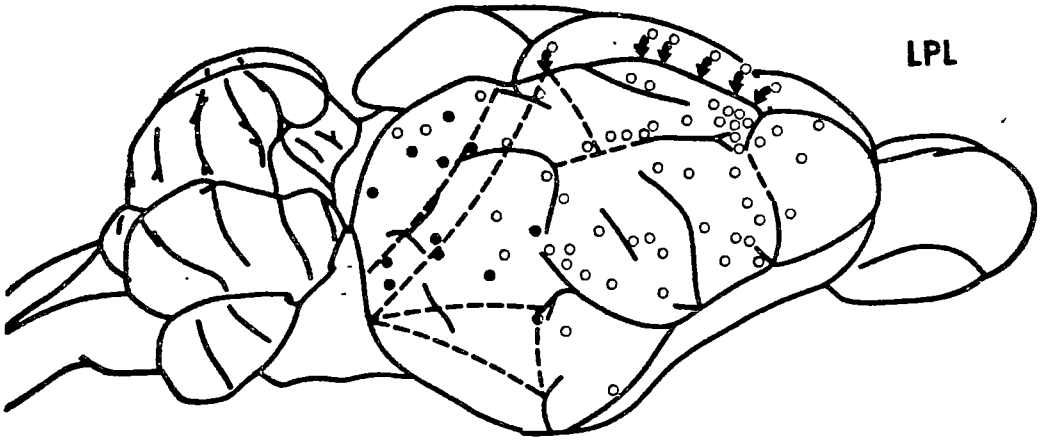
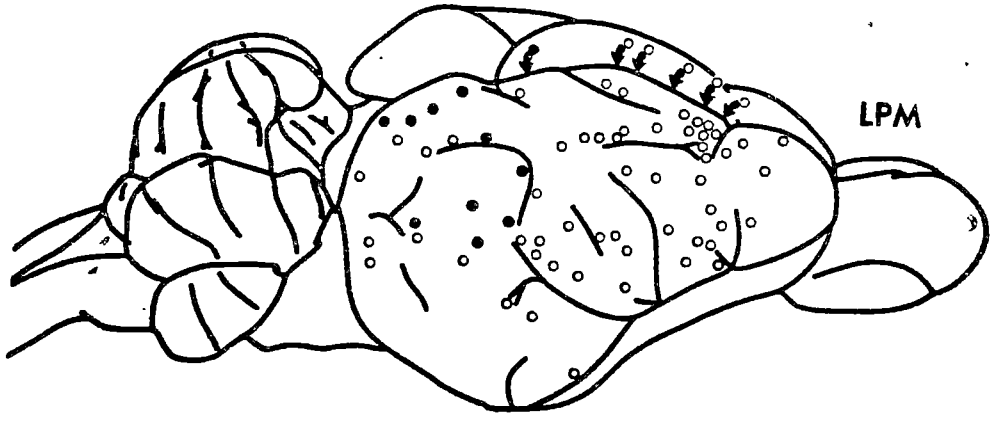


Figure 11

A. Cortical HRP injections in Trichosurus which resulted in retrograde labelling of the lateral division of the lateroposterior nucleus.



B. HRP injections which labelled the medial division of the lateroposterior nucleus.

(For further details see Haight et al 1980).

in that lateral parts of LP in both cases project preferentially to striate cortex. Apart from this the thalamocortical relationship of the regions clearly differ in important respects. This is not unexpected in view of the marked variation in tectal inputs previously mentioned.

Once more Trichosurus shows some general organisational similarities to the cat, since in these animals the medial tectorecipient zones of the LP-Pulvinar complexes project mostly (in the cat exclusively), to regions outside the striate area, while the lateral, non tectorecipient regions are heavily connected to striate cortex (Berson and Graybiel 1978, Haight et al 1980).

(iii) FUNCTIONAL CONSIDERATIONS

The variability seen in the organisation of input and output connections of the LP-Pulvinar group of different animals, and the great complexity of cortical relationships seen in some cases, particularly the cat and primates, makes analysis of the functions of these nuclei extremely difficult. That there is a primary role in the processing of visual information seems beyond question in view of the close relationships of the group with major visual centres. In part these nuclei presumably provide routes, via their tectal,

retinal, and pretectal inputs, by which visual information reaches various regions of cortex, and which are additional or alternate to retinogeniculo-cortical pathways and intrinsic corticocortical connections.

Some parts of the complex may be involved in cortico - thalamocortical loops, and thus provide pathways between different cortical regions in addition to the more direct corticocortical connections. This would presumably allow for more complex interactions between these regions (see Benevento and Davis 1977, Rezak and Benevento 1979 for recent discussions of this point).

LATERAL GENICULATE NUCLEI

(i) DESCRIPTIONS AND COMPARISONS OF NUCLEAR STRUCTURE IN MARSUPIALS

(a) DORSAL LATERAL GENICULATE NUCLEUS

(For illustrations see references below).

There is a wealth of information available on the cytoarchitecture of the dorsal lateral geniculate nucleus (LGd) in marsupials. LGd occupies the dorsolateral border of the caudal part of the thalamus, varying somewhat in relative rostrocaudal extent in different species, but in general being approximately coextensive with the medially adjacent lateroposterior nucleus (LP). In most species examined to date the nucleus is clearly divisible into an outer cell dense, laminated α segment, and an inner, relatively cell sparse, non laminated β segment, which may be difficult to differentiate from the adjoining LP. The two segments of the nucleus are in some cases separated by a distinct fibrous lamina. Exceptions to this basic plan include the grey kangaroo, in which both α and β segments display cellular laminae; the Virginia opossum (Didelphis) and common wombat, in which the α segment shows no obvious lamination; and some Australian

polyprotodont species, the Tasmanian devil and certain bandicoots, in which the LGd as a whole appears to be cytoarchitecturally homogeneous. In those species where cell laminae are evident the cytoarchitectural complexity of the nucleus varies considerably, even among closely related species. In general, however, the greatest complexity is seen in the diprotodonts, the more advanced of the two major marsupial groups, and in particular the larger macropods (kangaroos and wallabies) (American opossums; Lent, et.al. 1967, Oswaldo-Cruz and Rocha-Miranda 1967, Royce et al 1976: Australian polyprotodonts; marsupial mice and bandicoots, Sanderson et al 1983; Tasmanian devil, Sanderson et al 1979; native cat, Sanderson and Pearson 1977: diprotodonts; phalangers, Goldby 1941, Hayhow 1967, Johnson 1977, Johnson and Marsh 1969, Pearson et al 1976; koala, Haight and Nelson 1983; wombats, Sanderson and Pearson 1981, Sanderson et al 1983; kangaroos and wallabies, Sanderson et al 1983).

(b) VENTRAL LATERAL GENICULATE NUCLEUS

(For illustrations see Haight and Neylon 1978a figs 7-10, Haight and Neylon 1981b figs 7-9, Oswaldo-Cruz and Rocha Miranda 1967 figs 6-13).

Descriptions of the cellular organisation of the ventral lateral geniculate nucleus in marsupials are

limited in number, and provide details only for Didelphis (Lent et al 1976, Oswaldo-Cruz and Rocha-Miranda 1967) and for Trichosurus (Hayhow 1967). On the other hand, the distribution of afferent connections to this nucleus has been examined in several different species, and these provide some indication of its relative size and positional relationships (for references see following section). Taken together these studies show that the marsupial LGv is similarly located to that in most placental species, and is relatively large, with the cross sectional area in some cases approaching that of the dorsal nucleus. In Didelphis (Lent et al 1976) and Trichosurus (Hayhow 1967) LGv is broadly divisible into internal and external cell groups, similar to those found in placental animals (see Campbell 1972 and Niimi et al 1963 for reviews of placental LGv structure).

2. CONNECTIONS AND FUNCTIONS OF THE LATERAL GENICULATE NUCLEI

(a) DORSAL LATERAL GENICULATE NUCLEUS

(i) SUBCORTICAL AFFERENT CONNECTIONS

Placentals

The mammalian dorsal lateral geniculate nucleus (LGd) is the principal thalamic centre for the relaying of visual information to the cortex, and receives direct retinal projections from both eyes. The precise manner in which these projections are distributed within the nucleus varies considerably among different species. The basic mammalian arrangement generally involves the termination of retinal fibres in layers, with a varying, but generally considerable if not complete degree of separation of ipsilateral and contralateral inputs (see references below). Another common factor is that specific regions of the two retinae project in register, such that each point in the visual field can be represented as a line passing through the nucleus, perpendicular to the planes of the terminal laminae (Kaas et al 1972a).

The number of terminal laminae is variable in different

animals, as is the sequencing of, and numerical 'balance' between ipsilateral and contralateral layers, although general similarities are usually evident among members of particular mammalian groups. In most cases ipsilateral and contralateral input laminae alternate in at least part of the nucleus. In primates the numbers of laminae for each eye are (approximately) equal, while in other animals contralateral layers predominate.

Terminal laminae commonly correspond to distinct cell layers, however 'concealed' lamination of retinal terminals is not unusual, either within an apparently cytoarchitecturally homogeneous LGd, or within particular cell layers where these can be distinguished. In general, the degree of structural complexity of the nucleus, both in terms of cytoarchitecture and retinal projection patterns, is highest in those species with the greatest apparent need for rapid and accurate assessment of spatial relationships, such as arboreal animals, carnivores, and in particular primates (Campbell 1972, Kaas et al 1972a).

The functional significance of multiple inputs to LGd from the two eyes is not clear, although a number of possibilities have been suggested. The factors presently considered most likely to be responsible for

the development of geniculate layers are; that laminar thickness is limited by the need for binocular interactions within the nucleus; that interlaminar zones provide for cortical modulation of geniculate activity; and that different layers may relay information from different functional groups of retinal fibres (see Guillery 1979 and Kaas et al 1978 for recent discussions of these points). (For reviews of geniculate organisation see Campbell 1972, Guillery 1979, Kaas et al 1972a, 1978. For information on retinogeniculate projections in particular species or groups see: insectivores, Campbell et al 1967, Casagrande and Harting 1975, Hubel 1975, Lund and Lund 1965; bats, Cotter 1981, Cotter and Petney 1979, Petney and Cotter 1976, 1981; rodents, Cunningham and Lund 1971, Hayhow et al 1962, Mayner et al 1980, Tigges 1970, Weber et al 1977; lagomorphs, Giolli and Guthrie 1969, Takahashi et al 1977; ungulates, Campos-Ortega 1970, Cummings and de La Hunta 1969, Karamanlidis and Magras 1972, 1974; carnivores, Guillery 1970, Hayhow 1958, Hickey and Guillery 1974, Kaas et al 1972a, 1973, Sanderson 1974; primates, Kaas et al 1978).

In addition to direct retinal inputs, parts of LGd in some species have been shown to receive projections from the superficial layers of the superior colliculus (squirrel, Robson and Hall 1976; tree shrew, Albano et

al 1979, Fitzpatrick et al 1980, Harting et al 1973a; rat, Mackay-Sim et al 1983; cat, Graham 1977, Torrealba et al 1981; prosimian (Galago), Fitzpatrick et al 1980; monkeys, Harting et al 1978, 1980). It has been suggested that these regions of the geniculate may relay information from a particular group of small diameter visual fibres, both via direct retino-geniculate connections, and indirect retinocolliculo-geniculate connections, to the superficial laminae of the visual cortex (Fitzpatrick et al 1980, Harting et al 1978, 1980, Le Vay and Gilbert 1976, Weber et al 1983, Wilson and Stone 1975). Projections to LGd from the pretectum have also been reported in the rat (McKay-Sim et al 1983) and cat (Hughes and Chi 1981).

Significant inputs to LGd have also been reported in the rat and cat from a number of brainstem centres not usually considered to be associated with visual functions. These include the mesencephalic reticular formation, periaqueductal grey, and dorsal tegmental nucleus in the rat, and the raphe nuclei and locus coeruleus in the rat and cat (rat, MacKay-Sim et al 1983; cat, Leger et al 1975). These findings suggest that there may be extremely complex mechanisms available to modify visual information transfer through the geniculate nucleus.

Marsupials

The organisation of the primary visual pathways has been examined in a number of marsupials (American opossums, Lent et al 1976, Royce et al 1976: Australian polyprotodonts; native cat, Sanderson and Pearson 1977; Tasmanian devil, Sanderson et al 1979: diprotodonts; brush-tailed possum (Trichosurus), Hayhow 1967, Rockel et al 1972, Sanderson et al 1978, 1980; ring-tailed possum, Pearson et al 1976; hairy-nosed wombat, Sanderson and Pearson 1981; kangaroos and wallabies, Sanderson et al 1983). These studies show that while there is a high level of interspecies consistency in the patterns of retinal projections to most subcortical visual centres, the distribution pattern of retinal fibres in LGd varies considerably. In most animals examined to date these fibres terminate in clearly defined laminae, some of which may be 'concealed' within certain cell layers or regions which appear to be cytoarchitecturally homogeneous. The number and sequencing of the projection laminae can differ even among closely related species, as can the degree of binocular convergence in some parts of the nucleus. A significant degree of overlap of ipsilateral and contralateral inputs would appear to be a common, though perhaps not universal characteristic of the polyprotodonts, while segregation is more the rule

among diprotodont species. The most complex geniculate organisations are seen in the larger macropods (see Sanderson et al 1983).

Also of interest is the fact that in some diprotodont marsupials the number of ipsilateral projection laminae exceeds that of the laminae receiving contralateral inputs (Trichosurus, Hayhow 1967, Rockel et al 1972, Sanderson et al 1978; hairy nosed wombat, Sanderson and Pearson 1981; kangaroos, Sanderson et al 1983).

Projections to the thalamus from the superior colliculus have been examined using degeneration methods in Didelphis (Benevento and Ebner 1970, Martin 1969, Rafols and Matzke 1970) and Trichosurus (Rockel et al 1972). In neither animal have connections to LGd been reported.

Summary of Subcortical Afferent Connections and Comparison of Placental and Marsupial Organisation

Marsupials follow the basic mammalian plan in that projections from the two retinae terminate in laminae in LGd, however these animals display an even greater degree of interspecies variability in geniculate structure and retinal projection patterns than is evident among placentals. Some marsupials, and in particular the larger macropods, have extremely complex

geniculate organisations, similar to those seen in primates (Kaas et al 1978, Sanderson et al 1983). An important difference between some diprotodonts and placental animals is the presence of greater numbers of ipsilateral than contralateral projection laminae in the former group, while in placentals there are either equal numbers, or a majority of contralateral laminae.

Projections from the superior colliculus to parts of LGd, probably primarily via small diameter axons, would appear to be a common factor in placental animals. The fact that these have not been demonstrated by degeneration studies in marsupials may simply reflect the relative insensitivity of these methods.

(ii) CORTICAL RELATIONSHIPS

Placentals

In the placental animals examined to date, with the noteable exception of the cat, the available evidence indicates that geniculocortical projections are restricted entirely, or almost entirely to the primary visual area (VI, striate cortex, or area 17). Transneuronal tracer studies of retinocortical pathways in the tree shrew (Hubel 1975) and squirrel (Weber et

al 1977) have reported a limited spread of transported label beyond the boundaries of the striate area, however it is possible that this results from tracer being transferred via corticocortical connections, or indirect pathways via other thalamic regions, since other studies in the same animals provide evidence for geniculate connections to striate cortex only (tree shrew, Harting et al 1973b; squirrel, Kaas et al 1972b, Robson and Hall 1977). In the hedgehog (Gould et al 1978) and rabbit (Karamanlidis and Giolli 1977) LGd projections are probably limited to striate cortex. Despite some evidence to the contrary in the squirrel monkey (Wong-Riley 1976, but see also Tigges et al 1977) it is generally accepted that in primates geniculocortical fibres terminate only in the striate area (Garey and Powell 1971, Hendrickson et al 1978, Raczkowski and Diamond 1980, Rezak and Benevento 1979, Rowe et al 1978, Tigges et al 1977).

Projections of LGd to the immediate peristriate area, as well as striate cortex, have been reported in the sheep (Karamanlidis et al 1979) and rat (Coleman and Clerici 1980, Hughes 1977, Jones and Leavitt 1974, but see also Olavarria 1979), and may also be present in mice (Drager 1974), but these appear to be very limited in extent.

Among placentals only the cat has been shown to depart

radically from this common arrangement of restricted geniculate terminal fields. In this animal the nucleus is related to areas of visually responsive cortex extending well beyond the confines of the striate and immediate peristriate areas (Geisert 1980, Hollander and Vanegas 1977, Le Vay and Gilbert 1976, Marciewicz 1975, Niimi et al 1981b, Raczkowski and Rosenquist 1980, Rosenquist et al 1974).

The organisation of descending projections from the visual cortex in different animals indicates an essentially reciprocal relationship between the cortex and LGd (squirrel, Robson and Hall 1977; rabbit, Giolli and Guthrie 1971, Giolli and Pope 1973; cat, Kawamura et al 1974, Updyke 1975, 1977; primates, Campos-Ortega 1968, Graham 1982, Graham et al 1979, Hollander 1974, Lund et al 1975, Raczkowski and Diamond 1980, Spatz and Erdmann 1974).

LGd has been shown to be related in an orderly manner to the visual cortex in the hamster (Dursteler et al 1979), squirrel (Kaas et al 1972b) and primates (Cooper et al 1979, Rezak and Benevento 1979). In the cat not only are geniculocortical connections homotypically organised, but in addition different geniculate laminae are preferentially related to particular visual areas (Giesert 1980, Hollander and

Vanegas 1977, Le Vay and Gilbert 1976, Marciewicz 1975, Niimi et al 1981b, Rosenquist et al 1974).

In most or all placental species the majority of geniculocortical fibres probably terminate in lamina IV of visual cortex (hedgehog, Gould et al 1978; tree shrew, Hubel 1975; squirrel, Weber et al 1977; cat, Le Vay and Gilbert 1976; rhesus monkey, Rezak and Benevento 1979). In the tree shrew, cat and some primates projections have also been demonstrated to more superficial laminae, including lamina I, from those parts of LGd which receive inputs from the superior colliculus (cat, Le Vay and Gilbert 1976, Torrelba et al 1981; tree shrew and prosimian (Galago), Carey et al 1979, Fitzpatrick et al 1980; squirrel monkey, Weber et al 1983). Another basic similarity is evident among these animals, in that the terminals of pathways from the ipsilateral and contralateral retinae show a degree of separation within the visual cortex. These inputs may be directed either into different sublaminae, in the case of the tree shrew (Hubel 1975), or into radially oriented 'ocular dominance columns'. This latter organisation is particularly distinct in the rhesus monkey (Wiesel et al 1974) and other Old World primates (Hendrickson et al 1978), but has also been detected in the cat (Hubel and Wiesel 1965). Such segregation of visual inputs may not be common to all species with highly developed visual systems, however,

since it is not apparent in the squirrel (Weber et al 1977), or most New World monkeys (Hendrickson et al 1978, Rowe et al 1978).

Marsupials

Geniculocortical connections have been examined in some detail in both Didelphis and Trichosurus, and it is clear that their organisation differs markedly in the two species.

In Didelphis the LGd has been shown to project in an orderly pattern to the striate cortex only, and it would appear that the connections arise from the entire nucleus (Benevento and Ebner 1971, Coleman and Clerici 1981, Coleman et al 1977). On the other hand, however, descending fibres from the striate and peristriate areas appear to terminate primarily in the medial part of the nucleus (Benevento and Ebner 1970, Martin 1968).

The early retrograde degeneration study of geniculocortical connections in Trichosurus by Packer (1941) indicated an orderly relationship with the striate area only, however the application of the retrograde HRP tracer technique has revealed a very extensive LGd projection field which encompasses the striate, peristriate and posterior parietal areas. The

striate and peristriate areas receive homotypically organised projections arising mainly from the external laminated segment of the nucleus, while the medial non laminated segment projects, without any apparent ordering, mainly to the posterior parietal area (Haight et al 1980 and see fig 12). According to Rockel et al (1972), the striate and peristriate areas provide descending connections to both internal and external parts of the geniculate, however our material (Haight et al 1980) shows that the corticogeniculate and geniculocortical connections are essentially reciprocal.

The laminar distribution of geniculate inputs to the striate cortex in the two species is similar, with the main terminal area corresponding to layer IV. Minor connections to other laminae, including lamina I, have also been described in Didelphis (Benevento and Ebner 1971, Sanderson et al 1980).

A recent transneuronal tracer study of retinocortical pathways in Trichosurus (Sanderson et al 1980) indicates that inputs from the ipsilateral and contralateral retinae are not segregated into different sublaminae, or into 'ocular dominance' columns.

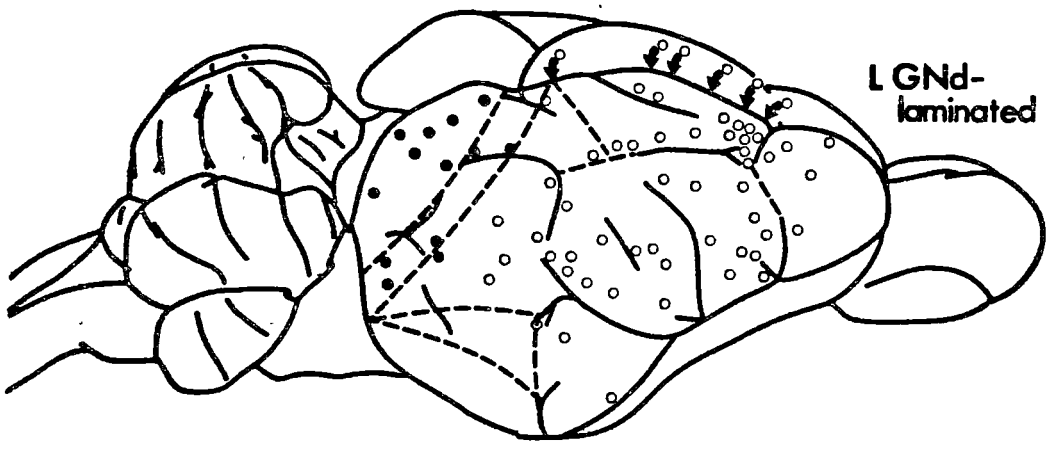
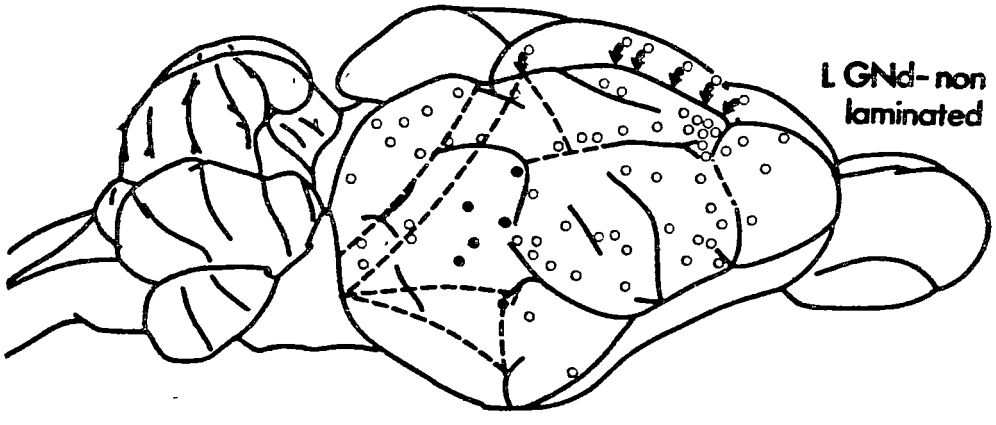


Figure 12

A. Cortical HRP injections in Trichosurus which produced retrograde labelling in the external laminated segment of the dorsal lateral geniculate nucleus (closed circles).



B. HRP injections which labelled the internal, non laminated segment of the dorsal lateral geniculate nucleus.

(For further details see Haight et al 1980).

Summary of Cortical Relationships and Comparison of Placental and Marsupial Organisation

Didelphis follows the same basic pattern of geniculocortical connections evident in almost all the placental species examined to date, where highly ordered projections are restricted entirely or almost entirely to the striate area.

Trichosurus, on the other hand, displays very distinct similarities to the cat. Both animals represent radical departures from the common mammalian plan in having geniculate projections to a large extent of the caudal cortical mantle. In addition, different nuclear laminae or groups of laminae have rather similar preferential relationships to particular areas of cortex in the two animals.

In the tree shrew, cat and Old World primates, inputs to the cortex from the ipsilateral and contralateral retinae show a degree of segregation. A similar arrangement is not evident in *Trichosurus*, the squirrel, or most New World monkeys, although these animals also have highly developed visual systems, as evidenced by the complex lamination of LGd.

In all species for which information is available, both placental and marsupial, geniculocortical projections

terminate mainly in lamina IV. In the tree shrew, cat and monkeys, particular geniculate laminae, and specifically those which receive projections from the superior colliculus, project to more superficial parts of the cortex, including lamina I. Whether a similar arrangement exists in other mammals is not known as yet, although the evidence for minor projections from the Didelphis LGd to superficial cortical laminae provides a hint that this may be the case.

(b) VENTRAL LATERAL GENICULATE NUCLEUS

(i) AFFERENT CONNECTIONS

Placentals

The ventral lateral geniculate nucleus, or pregeniculate nucleus of primates, varies in size in different placental groups, and is most prominent in the ungulates (Niimi et al 1963). In many species the nucleus is divisible into medial or internal, and lateral or external cell groups (Babb 1980, Campbell 1972, Niimi et al 1963). In some other animals, most notably the cat (Jordan and Hollander 1972), a more complex cellular organisation is evident.

Studies in a number of species, for the most part

utilising the anterograde degeneration method, have demonstrated bilateral, though predominantly contralateral, retinal projections restricted to lateral portions of the LGv, or equivalent parts of the primate pregeniculate nucleus (hedgehog and tree shrew, Campbell et al 1967; rat, Hayhow et al 1962; squirrels, Tigges 1970; rabbit, Giolli and Guthrie 1969; horse, sheep, pig and ox, Karamanlidis and Magras 1972, 1974; cat, Hayhow 1958; prosimian (Galago), Tigges and Tigges 1970; monkeys, Campbell 1972, Hendrickson et al 1970).

These studies may not have demonstrated the full extent of retinal projections in all cases. Other workers who have examined retinofugal pathways in the tree shrew (Laemle 1968), rat (Hickey and Spear 1976), Australian rodents (Mayner et al 1980), squirrels (Ablanalp 1974) and rabbit (Takahashi et al 1977), have recognised additional dorsally placed terminal layers, and, in the case of the rat, Australian rodents and rabbit, minor contralateral projections to medial parts of the nucleus. In the cat Hollander and Sanides (1976) found a very complex organisation of retinal projections to both medial and lateral parts of LGv. Anterograde tracer studies in bats (Cotter 1981, Cotter and Petney 1979) also demonstrate heavy projections to both medial and lateral parts of the nucleus, while an earlier degeneration study (Petney and Cotter 1976) had

indicated a more restricted input, mostly to lateral LGv.

These findings would suggest that, while lateral parts of LGv are probably the principle targets of retinal fibres in many species, they are not necessarily the sole terminal areas. The application of the more sensitive tracer techniques now available may reveal further cases where more extensive inputs are present than were formerly recognised.

In addition to retinal inputs LGv receives major projections from several other centres normally considered to be involved in visual functions, including the pretectal complex and superficial layers of the superior colliculus, the visual and adjacent areas of cortex, parts of the accessory optic system and the opposite LGv. Examination of the results of those studies in which the locations of different terminal fields are identified (references marked * below) reveals a number of interspecies and interstudy differences.

In view of these inconsistencies, and the question already raised as to the total extent of retinal projections to LGv, it is not at this stage possible to determine with any certainty the degree of overlap, and hence interaction, of the various visual system inputs,

or whether any common organisational plan or plans exist (pretectal projections: tree shrew, Weber and Harting 1980*; rat, Mackay-Sim et al 1983; cat, Berman 1977*, Hughes and Chi 1981, Itoh 1977*; rhesus monkey, Benevento et al 1977: collicular projections: hedgehog, Hall and Ebner 1970; tree shrew, Albano et al 1979, Harting et al 1973a; rat, Mackey-Sim et al 1983, Perry 1980*; squirrel, Ablanalp 1970*, cat, Graham 1977*, Hughes and Chi 1981; rhesus monkey, Benevento and Fallon 1975, Harting et al 1980: cortical projections: tree shrew, Ablanalp 1970*, Harting and Noback 1971*, squirrel, Ablanalp 1970*; rabbit, Giolli and Guthrie 1971*; cat, Hughes and Chi 1981, Kawamura et al 1974*, Updyke 1977, 1981*; marmoset, Spatz and Erdmann 1974, Spatz and Tigges 1973*; prosimian (Galago), Campos-Ortega 1968; monkeys, Campos-Ortega et al 1970b, Graham et al 1979, Hollander 1974, Ogren and Hendrickson 1976: projections from accessory optic system and contralateral LGv: rat, Mackey-Sim et al 1983; cat, Hughes and Chi 1981).

Projections to LGv have also been reported from a number of 'non visual' brainstem centres in the rat (Graybiel 1974, Mackey-Sim et al 1983) and cat (Hughes and Chi 1981), including the dorsal raphe nucleus and locus coeruleus (rat and cat) and the cerebellum, mesencephalic reticular formation, periaqueductal grey

and dorsal tegmental nucleus (rat).

Marsupials

The distribution of retinal connections to LGv is very similar in the marsupials examined to date, and basically corresponds to that described in most placental species. The contralateral retina projects heavily to lateral parts of the nucleus, overlapping a smaller ipsilateral input. In addition, however, a thin dorsal leaflet of retinal terminals is evident in all animals. This region may be comparable to the similarly located regions referred to previously (see above) in the tree shrew, rat, Australian rodents, squirrels and rabbit (American opossums, Lent et al 1976, Royce et al 1976; Australian polyprotodonts, Sanderson and Pearson 1977, Sanderson et al 1979; diprotodonts, Hayhow 1967, Pearson et al 1976, Rockel et al 1972, Sanderson and Pearson 1981, Sanderson et al 1978, 1983).

Projections to LGv from the pretectal region (Benevento and Ebner 1970) and cerebellum (Martin et al 1974) have been reported in Didelphis, and from the superior colliculus and visual cortex in Didelphis (Benevento and Ebner 1970, Martin 1968, 1969, Rafols and Matzke 1970) and Trichosurus (Haight et al 1980, Rockel et al 1972). In Trichosurus it would appear that these

inputs terminate in different parts of the nucleus, with cortical projections extensively overlapping the laterally placed retinal field (Rockel et al 1972). In Didelphis, too, cortical fibres are distributed mainly to the lateral part of the nucleus (Benevento and Ebner 1970).

(ii) EFFERENT CONNECTIONS

No evidence is available to suggest that LGv projects to the cortex in any mammal, however the nucleus has been shown in the rat and cat to have a wealth of subcortical connections (rat, Graybiel 1974, Legg 1979, Swanson et al 1974; cat, Edwards et al 1974, Kawamura et al 1978, Swanson et al 1974). These for the most part are directed to those regions from which the LGv receives inputs, or to regions which also receive inputs from other major visual centres or pathways.

Thus, connections to the pretectal complex terminate in those divisions which receive retinal inputs, while those to the superior colliculus terminate in the layers which receive visual cortical projections. LGv also projects to the contralateral LGv, to the lateral terminal nucleus of the accessory optic system and suprachiasmatic nucleus, and to the centrolateral thalamic nucleus, which has been implicated in

visuomotor functions (Hunsperger and Roman 1967, Schlag et al 1974).

'Non visual' targets include the subthalamus, pontine grey, periaqueductal grey and perirubral field.

No information is available on LGv efferent connections in marsupials, however the similarities seen between the cat and rat would suggest that comparable organisations may be present in most or all mammalian species.

(iii) FUNCTIONAL CONSIDERATIONS

The close and complex relationships, some of them reciprocal, between LGv and the major visual centres or pathways, or regions involved in visuomotor activities (including the cerebellum), strongly suggest an important role or roles for the nucleus in such functions (Kawamura et al 1978). Physiological and behavioural studies provide support for involvement of the nucleus in visuomotor activity (Buttner and Fuchs 1973) and light intensity discrimination (Legg and Cowey 1977). Relationships with 'non visual' centres may be concerned with regulatory mechanisms modulating general thalamic activities (Mackay-Sim et al 1983).

MEDIAL GENICULATE NUCLEUS

(i) DESCRIPTIONS AND COMPARISONS OF NUCLEAR STRUCTURE IN MARSUPIALS

(For illustrations see Aitken and Gates 1983 figs 2, 3, Haight and Neylon 1978a figs 10, 11, Haight and Neylon 1981a figs 10-12, Oswaldo-Cruz and Rocha-Miranda 1967 figs 11-14), Rockel et al 1972 figs 1, 2).

The marsupial medial geniculate nucleus (MG) is a prominent feature of the caudal lateral thalamus, extending from a level near the caudal pole of the ventroposterior complex to the caudal limit of the thalamus.

The nucleus exhibits an extremely complex internal organisation. Bodian (1939) recognised two main components of the Didelphis MG, which he referred to as the 'marginal' and 'central' divisions, with the latter containing more closely packed, darker staining cells. He considered these regions to be the probable equivalents of the 'principal' and 'magnocellular' divisions respectively of MG described by Rioch (1929) in the cat. Oswaldo-Cruz and Rocha-Miranda (1967) later followed Bodian's treatment in their description of the Didelphis thalamus, although they found it

difficult to distinguish between the two regions.

In Trichosurus Rockel et al (1972) also recognised two main portions of MG; an externally and caudally placed 'principal', and a rostral medial 'internal' division, which they felt were probably equivalent to the regions so named by Tarlov and Moore (1966) in the rabbit, and similar to Bodian's two subnuclei in Didelphis.

We followed the example of Rockel's group in our descriptions of the Trichosurus and Dasyurus thalami (Haight and Neylon 1978a, 1981a). Recently Aitkin and Gates (1983) have made a more detailed analysis of the cellular organisation of the Trichosurus MG, in which they apply a somewhat different parcellation system. They reported that the cytoarchitecture of the nucleus is extremely complex, and found some difficulty in recognising distinct and consistent subdivisions. They did not accept the treatment of Rockel's group, but suggested that the nucleus is best considered as comprising three main segments; a non homogeneous dorsomedial part, and lateral and medial parts. These they felt to be similar to the dorsal, ventral, and medial or magnocellular subdivisions respectively of the cat MG (Morest 1964 and see also Niimi and Kuwahara 1973).

It should be noted that whichever parcellation system proves to be the more appropriate, neither fully represents the extremely complex structure of the nucleus. Examination of thalamic sections of Trichosurus, Dasyurus, and Didelphis (and see also Aitkin and Gates 1983 fig 3) reveals a number of very small but distinct zones in different parts of MG, whose cells often differ markedly in size or shape from those in neighbouring regions. These foci are scattered, but are evident mostly in external parts of the nucleus. They often do not appear to be consistent from one animal to another, however, or even between one side and the other in the same animal. What significance these numerous cell groups in MG may have in terms of the connections and functions of the nucleus remains to be seen.

2. CONNECTIONS AND FUNCTIONS OF THE MEDIAL GENICULATE NUCLEUS

Placentals

The medial geniculate nucleus or body is the principal thalamic centre for relaying auditory information to cortex. The main subcortical inputs to the nucleus originate in the inferior colliculus. Early degeneration studies of inferior colliculus projections

to MG in the cat and monkey indicated that dorsal caudal parts of the nucleus received few if any terminals (cat, Moore and Goldberg 1963, Powell and Hatton 1969; monkey, Moore and Goldberg 1966). Recent tracer studies in the cat (Anderson et al 1980a, Kudo and Niimi 1978) and tree shrew (Casseday et al 1976) have shown that the pericentral nucleus of the inferior colliculus projects in part to this region. This and other parts of MG also receive connections from the lateral midbrain tegmentum (cat, Morest 1965b; tree shrew, Oliver and Hall 1978a). The functional significance of these tegmental inputs remains unclear (see Oliver and Hall 1978a).

Anderson et al (1980a, b) have recently presented evidence for two largely segregated systems of auditory projections to cortex in the cat. One, a receptotopically organised pathway, relays via the central nucleus of the inferior colliculus primarily to rostral and medial parts of MG, and from these to the primary and other receptotopically organised areas of auditory cortex. The other involves connections via the pericentral nucleus of the inferior colliculus, and medial and dorsocaudal parts of MG, mostly to the secondary auditory area. This pathway is apparently not receptotopically organised. Connections of the medial or magnocellular division of the medial geniculate nucleus are involved in both systems. These

authors also reported that connections between particular parts of MG and auditory cortex are essentially reciprocal. Their findings are supported by earlier studies of auditory pathways in this animal (Kudo and Niimi 1978, Niimi and Matsuoka 1979, Pontes et al 1975, Winer et al 1977).

Auditory pathways in the tree shrew would appear to parallel those in the cat in most respects, though they may have a more complex organisation (Casseday et al 1976, Oliver and Hall 1978 a,b).

Projections from various somesthetic pathways and centres to parts of the medial or magnocellular division of MG have been reported in some animals. These regions are more appropriately considered as parts of the posterior nucleus or complex (see Neylon and Haight 1983). In the cat at least, these somesthetic connections show little if any overlap with those of the auditory pathways (Niimi and Matsuoka 1979).

Marsupials

Degeneration studies of inferior colliculus projections in Didelphis (Martin 1969) and Trichosurus (Rockel et al 1972) produced results comparable to similar studies

in the cat and monkey (Moore and Goldberg 1963, 1966, Powell and Hatton 1969), in that projections to rostral parts of MG were very heavy, but the caudal pole of the nucleus appeared to be essentially terminal free. Rockel et al (1972) did, however, find evidence for a projection from the lateral midbrain tegmentum to caudal MG. It seems likely from these findings that the input connections of the marsupial MG are organised in a manner similar to those of placental species.

Early retrograde degeneration studies in Didelphis (Bodian 1942, Diamond and Utley 1963) and Trichosurus (Goldby 1943) outlined the areas of temporal cortex receiving MG projections, which are similarly located in the two animals, but did not provide any details of the organisation of these projections.

Aitkin and Gates have recently examined the functional organisation of the auditory cortex, and the arrangement of ascending projections from MG in Trichosurus (Aitkin and Gates 1983, Gates and Aitkin 1982). They demonstrated that the auditory cortex is receptotopically organised, although along somewhat different lines to the auditory areas of the placental species examined to date (squirrel, Merzenich et al 1976; cat Reale and Imig 1980; monkeys, Imig et al 1977, Merzenich and Brugge 1973), and found indications for orderly projections from part at least (their

lateral division) of MG to cortex. Their anatomical data are too limited to provide a basis for detailed comparison with other animals, however in the cat the lateral (ventral) region of MG forms part of the receptotopically organised auditory pathway described by Anderson et al (1980a, b).

We have some limited information on MG projections to cortex from our HRP studies in Trichosurus (fig 13). These suggest possible differential relationships between medial and lateral parts of the nucleus, and medial (dorsal) and lateral (ventral) parts of the auditory area (Haight et al 1983 and see Neylon and Haight 1983 fig 7), which would appear to be in general agreement with the findings of Aitkin and Gates (1983).

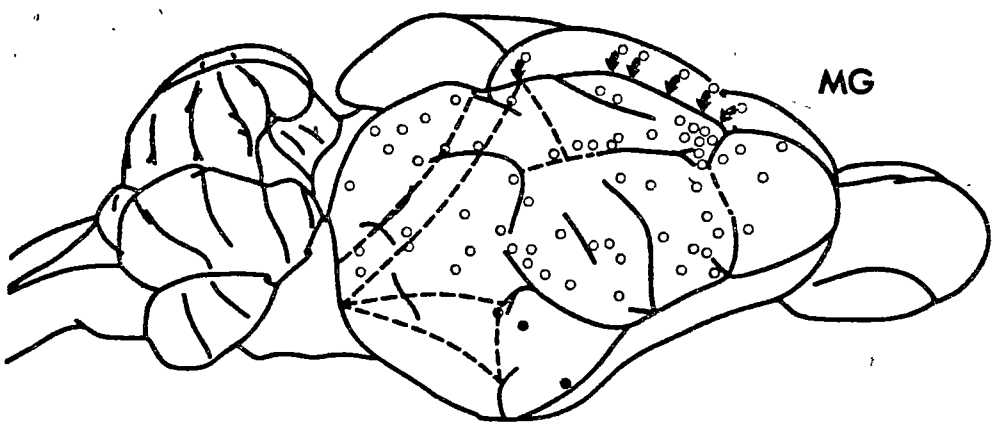


Figure 13

Cortical HRP injections in Trichosurus which produced retrograde labelling in the medial geniculate nucleus (closed circles).

NUCLEI OF THE CAUDAL THALAMUS

Four centres located in the caudal thalamus remain to be considered. These are the posterior, suprageniculate, extrageniculate, and subparafascicular nuclei. They are treated together because of their close positional relationships, and also for convenience. In addition three of the four nuclei demonstrate certain functional similarities.

1. DESCRIPTIONS AND COMPARISONS OF NUCLEAR STRUCTURE IN MARSUPIALS

(a) POSTERIOR NUCLEUS

(For illustrations see Haight and Neylon 1981a figs 6-12, Neylon and Haight 1983 figs 4-6).

The posterior nuclei (PO) of *Trichosurus* and *Dasyurus* are very similar in cytoarchitecture and location. Some difficulties are encountered when these animals are compared with *Didelphis*. These relate to the various systems of nomenclature and nuclear parcellation applied by different workers to a region which appears to be essentially similar to the PO of the two Australian species.

In our original description of the Trichosurus thalamus (Haight and Neylon 1978a) we considered that PO corresponded closely to the region designated by Rockel et al (1972) as the 'lateralis B' (after Goldby 1941) component of their posterior nuclear complex. Further consideration of thalamic cytoarchitecture, and the organisation of input and output connections of the caudal thalamus in this and other species, later led us to extend PO caudally. This new caudal part of PO comprises regions previously included within the suprageniculate (SG) and subparafascicular (SPF) nuclei, located at the medial margin of the medial geniculate nucleus (Neylon and Haight 1983).

PO in Dasyurus has less distinct boundaries than in Trichosurus, but has very similar structure and positional relationships (Haight and Neylon 1981a).

From examination of available Didelphis material it is clear that a region with similar cellular organisation, though rather indistinct boundaries, occupies much the same position as PO in Trichosurus and Dasyurus. This region corresponds to the nucleus C, the caudal part of the ventrolateral nucleus, and probably to part at least of the posterior nucleus of Oswaldo-Cruz and Rocha-Miranda (1967). Killackey and Ebner (1972) included Oswaldo-Cruz and Rocha-Miranda's nucleus C and

caudal VL, together with parts of the traditionally defined central intralaminar group, in a region they designated as the 'central intralaminar nucleus' or 'CIN'. We have recently presented arguments for considering the Didelphis 'CIN' both structurally and functionally equivalent to PO in Trichosurus and Dasyurus, and to parts of the posterior nuclear complex in placental species, and for considering the term 'PO' to be the more appropriate (Neylon and Haight 1983).

(b) SUPRAGENICULATE NUCLEUS

(For illustrations see Haight and Neylon 1981a figs 9-12, Neylon and Haight 1983 figs 4-6, Oswaldo-Cruz and Rocha-Miranda 1967 figs 11-14).

The suprageniculate nucleus (SG) is similar in the three marsupials, but most easily distinguished in Trichosurus. Caudally the nucleus forms a wedge of cells at the dorsomedial aspect of the medial geniculate nucleus, dorsal to the caudal extension of PO. At more rostral levels SG shifts medially, and is interposed between the expanding lateroposterior nucleus and the pretectal nucleus, and is separated from PO by the fibres of the medial lemniscus.

In our examination of the structure and connections of SG in Trichosurus (Neylon and Haight 1983) we removed a

small region originally included as the ventromedial portion of caudal SG (see Haight and Neylon 1978a), to place it within the caudal extension of PO. Otherwise SG corresponds to the suprageniculate nucleus as described by Goldby (1941) and to the suprageniculate component of the posterior complex (POs) of Rockel et al (1972).

Bodian (1939) and Oswaldo-Cruz and Rocha-Miranda (1967) recognised SG as a separate structure in Didelphis. Later studies have included the SG region in a larger 'posterior nucleus' (Coleman and Clerici 1981, Coleman et al 1977, Diamond and Utley 1963, Donoghue and Ebner 1981a, Pubols 1968).

(c) EXTRAGENICULATE NUCLEUS

(For illustrations see Haight and Neylon 1978a figs 8-10, Haight and Neylon 1981a fig 10).

The extrageniculate nucleus (EG) is a small and indistinct cell group in the caudal thalamus. Its presence was initially noted in Trichosurus, where it is distinguished from adjacent nuclei more by the distribution of its cortical projections than by distinctive cytoarchitecture (Haight and Neylon 1978a, Haight et al 1983). Similarly, EG in Dasyurus is

identifiable primarily by its distinctive cortical connections (Haight and Neylon 1981a, b).

In coronal sections of the thalamus in these two animals the rostral pole of EG appears as a crescent of cells ventral to the lateroposterior nucleus, between the fibres of the medial lemniscus and those of the external medullary lamina and optic tract. At more caudal levels EG encapsulates the lateral surface of the rostral pole of the medial geniculate nucleus (MG). At most levels EG can be seen to be in continuity with VPL beneath the fibres of the medial lemniscus.

In horizontal sections of the Trichosurus thalamus the nucleus is more easily distinguished, and at some levels its rostral pole is clearly continuous with VPL through a gap in the medial lemniscus. The impression one obtains is that EG may be a lamina of VPL cells cut off for the most part from the remainder of the nucleus by the medial lemniscus and the rostral pole of MG, a view not inconsistent with the organisation of its cortical projections (see below).

In the coronally sectioned Didelphis thalami available for examination, a region similar to EG in the other two species could be seen. Positive identification is not possible, due to of the lack of distinction between this region and adjacent nuclei, the non availability

of horizontally sectioned material, and a lack of detailed information on the connections of this part of the thalamus.

In the rat Feldman and Kruger (1980) have described a cell group with very similar positional relationships to EG (their intermediate geniculate nucleus or IG). The afferent connections of this centre would also suggest equivalence with the marsupial nucleus (see below). No similar region has been described in any other species to date.

(d) SUBPARAFASCICULAR NUCLEUS

(For illustrations see Haight and Neylon 1978a figs 8-11, Haight and Neylon 1981a figs 9-12, Neylon and Haight 1983 figs 4,5, Oswaldo-Cruz and Rocha-Miranda 1967 figs 11-14).

The subparafascicular nucleus (SPF) is very similar in the three marsupials being considered. Rostrally, the nucleus appears as a compact group of cells beneath the parafascicular nucleus and adjoining the medial margin of the ventroposterior nuclei (VP). At more caudal levels SPF shifts laterally while maintaining its relationship with the diminishing VP complex, until with the disappearance of the latter it lies at the

ventromedial aspect of the medial geniculate nucleus (MG), a position it holds almost to the level of the caudal pole of MG.

As presently delineated, SPF in Trichosurus differs slightly from the nucleus as described by Goldby (1941) and ourselves (Haight and Neylon 1978a). A small dorsal portion of caudal SPF has been reassigned to PO (see Neylon and Haight 1983).

In Didelphis recent studies of thalamic connections have included the caudal part of SPF, where it lies adjacent to MG (see Bodian 1939, Oswaldo-Cruz and Rocha Miranda 1967), within a posterior nucleus, a grouping which also incorporates the suprageniculate nucleus (Coleman and Clerici 1981, Coleman et al 1977, Diamond and Utley 1963, Donoghue and Ebner 1981a, Pubols 1968, Walsh and Ebner 1973).

2. CONNECTIONS AND FUNCTIONS OF NUCLEI OF THE CAUDAL THALAMUS

(a) POSTERIOR NUCLEUS

(i) SUBCORTICAL AFFERENT CONNECTIONS

Placentals

Regions designated as the posterior nucleus, or as a posterior nuclear complex, have been recognised in a number of placental species (e.g. tree shrew, Schroeder and Jane 1971; cat, Poggio and Mountcastle 1960, Rose and Woolsey 1958; primates, Burton and Jones 1976, Pearson and Haines 1980a, b, Whitlock and Perl 1961) The use of these terms to refer to regions of the caudal thalamus with similar locations and connections in different animals is, however, by no means universal. Examination of the literature pertaining to the structure and connection of these regions reveals considerable interstudy variation in the placement of nuclear boundaries and of nomenclature. Despite these problems it is clear that in many animals a region related to the medial border of the medial geniculate body, and to the dorsal aspect of the ventroposterior complex, regardless of what it is called, receives projections from the spinal cord, and dorsal column and

trigeminal nuclei. Furthermore, it appears that there is some differentiation between the distribution of trigeminal and other somesthetic pathway inputs, with the former being directed primarily to more medially placed parts of the total projection field (hedgehog, Jane and Schroeder 1971; rat, Lund and Webster 1967a,b, Feldman and Kruger 1980; cat, Berkley 1980, Burton et al 1979, Jones and Burton 1974, Jones and Powell 1971; tree shrew, Schroeder and Jane 1971; prosimian (Galago), Pearson and Haines 1980a; monkeys, Berkley 1980, Boivie 1978, 1979, Ganchrow 1978, Smith 1975, and see Mehler 1969 for rat, cat and monkey).

In addition to these inputs from the major somesthetic pathways or centres, a rostrolateral portion of the thalamic region in question has been shown by some authors (Donoghue et al 1979, Faull and Carman 1978), but not others (Haroian et al 1981), to receive cerebellar projections in the rat. In the cat and monkeys the weight of evidence would suggest that such projections are not present (Angaut and Bowsher 1970, Hendry et al 1979, Kalil 1981, Kievit and Kuypers 1972, Miller and Strominger 1977, Percheron 1977, but see Berkley and Mash 1977 for cat).

Finally, projections from the inferior colliculus to a region referred to as the lateral divison of the

posterior complex, which lies adjacent to the medial geniculate nucleus, have been reported in the cat (Moore and Goldberg 1963, Anderson et al 1980a), but not the rhesus monkey (Moore and Goldberg 1966). A projection from the superior colliculus to the region immediately dorsal to VPM, and which probably corresponds to part of PO, is suggested by the degeneration study of Niimi et al (1970) in the cat, but not supported by the data presented in the more recent autoradiographic study by Graham (1977). No obvious parallels for such connections are evident from studies of superior collicular projections in other placental species (tree shrew, Harting et al 1973a; hedgehog and bushbaby, Harting et al 1972; monkey, Harting et al 1980).

Marsupials

Rockel et al (1972) showed that the spinal cord and dorsal column nuclei in Trichosurus project to a region extending from the medial border of the medial geniculate nucleus (MG) to the dorsolateral aspect of the ventroposterior complex (VP). This region corresponds to caudal and lateral parts of the posterior nucleus (PO) as presently delineated in this animal (Neylon and Haight 1983).

In addition to the abovementioned inputs, the data

presented by Rockel's group (1972) suggest the possibility of a trigeminal projection to the medial part of PO. These authors also reported a projection to this same general area from the superior colliculus, while a caudal part of PO was found to receive inferior collicular connections. They found no evidence for cerebellar projections to PO, however we have some (Haight and Neylon unpublished observations) evidence to suggest that such an input is present.

In Didelphis a region extending from the medial border of MG, to the dorsal aspect of VP, which corresponds largely to the region designated as 'Central Intralaminar Nucleus' or 'CIN' by Killackey and Ebner (1972), but also to parts of the posterior nucleus of other authors, has been shown to receive projections from the spinal cord, dorsal column nuclei, and very likely the trigeminal nuclei, with these latter connections apparently being preferentially directed to more medial portions of the total projection field (Hazlett et al 1972, Walsh and Ebner 1973, Mehler 1969). Cerebellar inputs to part of the region in question have also been demonstrated (Martin et al 1974, Walsh and Ebner 1973). No evidence has been found for any connections to these areas of the thalamus from either the superior or inferior colliculi (Martin 1969).

Summary of Subcortical Afferent Connections and Comparison of Placental and Marsupial Organisation

Despite considerable differences in nomenclature and nuclear parcellation as presented in different studies, it seems clear that a region related to the medial border of MG, and to the dorsal surface of VP, receives a similar pattern of spinal, dorsal column lemniscal, and trigeminal projections in all the mammalian species examined to date. In *Didelphis*, and probably in *Trichosurus* and the rat, but not the cat and monkey, part of PO or its equivalent also receives cerebellar projections. Projections from the inferior colliculus to the caudolateral part of PO, as reported in *Trichosurus*, may correspond to projections to the region designated as the lateral division of the posterior complex in the cat. In *Didelphis*, and in the rhesus monkey, similar projections are not evident. The connections reported in *Trichosurus* from the superior colliculus to the medial part of PO may not be present in other species.

(ii) CORTICAL RELATIONSHIPS

Placentals

The region designated as the medial division of the posterior nuclear complex (Pom) in the rat, mouse, and the prosimian, Galago, has been shown to project extensively to the primary sensory, or sensorimotor cortex (Donoghue et al 1979, Herkenham 1980, Pearson and Haines 1980b, White and De Amicis 1977). In the rat there is some evidence for a point to point organisation of these projections, with the hindlimb cortex being related to the lateral part, and the head sensory area to the medial part of POm (Donoghue et al 1979).

In monkeys POm, which is apparently equivalent in terms of somesthetic pathway inputs to similarly located regions in other species, appears to have no projections to primary somatosensory cortex (Burton and Jones 1976, Jones et al 1979, Strick 1975, 1976a), but is connected to more caudally placed areas (Burton and Jones 1976). Early studies in the cat suggested a similar organisation (Graybiel 1973, Heath and Jones 1971, Jones and Leavitt 1973). More recently, substantial evidence has been presented for significant projections from POm to the primary somatosensory area (Bentivoglio et al 1978, Spreafico et al 1981), as well

as to more caudal cortex (Tanji et al 1978). POm in the cat also receives descending projections from somatosensory cortex (Jones and Burton 1974).

The region designated as the lateral division of the posterior complex (POl) in the cat, receives inputs from the inferior colliculus (Anderson et al 1980a, Moore and Goldberg 1963), and projects to auditory and adjacent regions of cortex (Anderson et al 1980b, Jones and Leavitt 1973). Burton and Jones (1976) recognised a centre which projects to regions adjoining auditory cortex in monkeys, which they also referred to as the lateral division of PO, however this region apparently lacks inferior collicular projections (Moore and Goldberg 1966)

Marsupials

In Trichosurus PO projects widely to the parietofrontal (sensorimotor) and posterior parietal cortex (fig 14a), and in turn receives descending connections from these regions. PO-cortical connections exhibit a point to point organisation, with the body and limb sensorimotor area and posterior parietal area, and the head sensory area, being related to lateral, including the caudal extension, and to medial parts of the nucleus respectively (Neylon and Haight 1983). In Dasyurus,

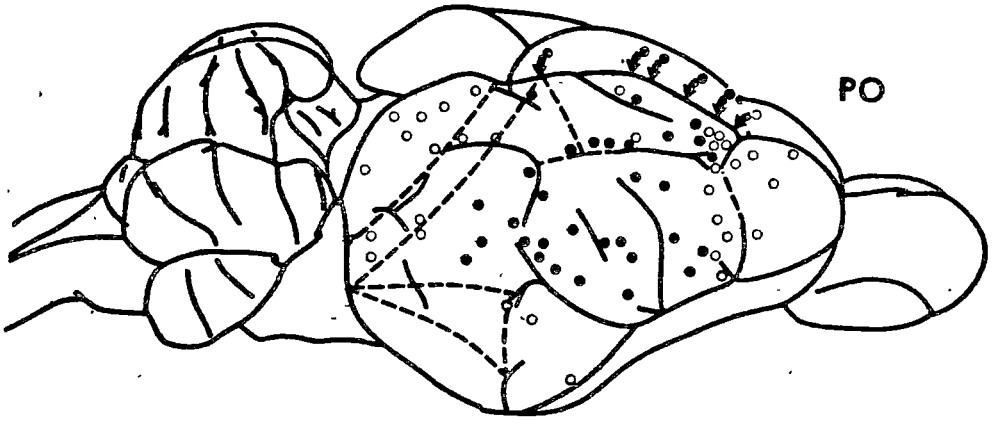
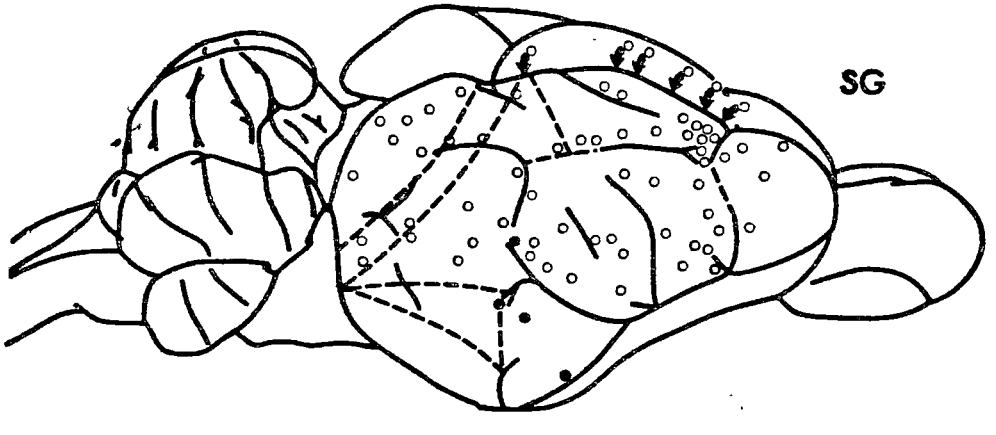


Figure 14

A. Cortical HRP injections in Trichosurus which produced retrograde labelling in the posterior nucleus (closed circles).



B. HRP injections which labelled the suprageniculate nucleus.

(For further details see Neylon and Haight 1983).

too, PO projects to the parietofrontal area, with an apparently similar differential distribution of connections from medial and lateral parts of the nucleus. No information is available as yet on possible connections to posterior parietal cortex in this animal (Haight and Neylon 1981b).

The region designated as 'CIN' in Didelphis is connected extensively and reciprocally to parietofrontal or sensorimotor and posterior parietal cortex (Donoghue and Ebner 1981a, Killackey and Ebner 1972, 1973). Lateral parts of 'CIN' appear to be preferentially related to the body sensorimotor area and the posterior parietal area, and medial 'CIN' to head sensorimotor cortex (Donoghue and Ebner 1981a). As previously stated, this region appears to be equivalent, in position and afferent connections, to the Trichosurus PO.

Summary of Cortical Relationships and Comparison of Placental and Marsupial Organisation

The distribution of projections from PO, or its equivalent, to somatic sensory or sensorimotor and posterior parietal cortex would appear to be common to a number of marsupial and placental species, with the exception of certain advanced primates, where such

projections appear to be restricted to regions caudal to somatosensory cortex. In the three marsupials under examination, and in the rat, a similar point to point organisation of thalamocortical connections is evident.

Caudal and lateral parts of PO in Trichosurus, which according to Rockel et al (1972) receive inferior collicular as well as somesthetic projections, project in part to regions of the posterior parietal area adjoining auditory cortex. This may represent a parallel organisation to projections from the so called lateral divisions of the posterior complex in cats and monkeys, to regions adjacent to the auditory area. In the cat, however, but not Trichosurus, this region is also related to auditory cortex, and in the monkey inferior collicular inputs are apparently lacking. It seems likely therefore, on the basis of the present evidence, that the regions in question are probably not fully equivalent in these animals.

(iii) FUNCTIONAL CONSIDERATIONS

The main input connections of PO in Trichosurus, and of similarly located centres in other species, come from the major somesthetic pathways. In most of the animals examined to date the ascending projections of this thalamic region terminate in large part in the somatic sensory or sensorimotor cortex. In some animals there

is evidence for a functional division of the region into medial and lateral parts, with the former apparently being primarily concerned with somesthetic information from the head, and the latter with body information.

The presence of major spinothalamic projections to PO, and the reported physiological properties of neurons in the region, led in the past to the suggestion of an important role in pain transmission (Poggio and Mountcastle 1960). Other evidence suggestive of such a role may be found in the recent report by Lewis et al (1983), that there is a close correspondence between the laminar distributions of opiate receptors and of PO terminals in the rat sensory motor cortex. On the other hand, Donoghue and Ebner (1981b), on the basis of their own and others (Sousa et al 1971) physiological findings in Didlephis, have suggested that the region may be a relay for deep somesthetic information. In addition, Robinson and Burton (1980) have shown that neurons in the PO(m) cortical projection field in monkeys responded preferentially to light mechanical rather than noxious stimuli.

Donoghue and Ebner (1981b) showed that the Didelphis 'CIN' (=PO) projects to lamina I of the cortex, which

would suggest some role in modifying or modulating cortical responses to thalamic projections to deeper layers, presumably from such centres as the ventroposterior complex. In the rat, too, PO has been shown to project heavily to lamina I, although in this animal additional inputs are present to deeper layers, with the levels varying in different regions of cortex (Herkenham 1980). It is of interest that the cortical projections of the ventromedial nucleus (VM), which in most animals terminate mainly in rostral areas of the cortex, are distributed primarily to layer I (Divac and Passingham 1980, Glenn et al 1982, Herkenham 1979). PO and VM may then perform somewhat similar functions in different regions of cortex.

Until further information becomes available, however, the only definitive functional role that can be assigned to PO is the relaying of somesthetic information to cortex.

(b) SUPRAGENICULATE NUCLEUS

(i) SUBCORTICAL AFFERENT CONNECTIONS

As with the posterior nucleus, the thalamic region most commonly referred as the suprageniculate nucleus (SG) has suffered a variety of treatments by different authors, both in terms of placement of nuclear

boundaries and of nomenclature. This creates problems in making interspecies and interstudy comparisons. Despite these difficulties, however, it is apparent that SG, or an equivalent region in the cat, tree shrew and rhesus monkey, receives strong projections from the deeper layers of the superior colliculus (Benevento and Fallon 1975, Graham 1977, Harting et al 1973a). In other species, including Didelphis and Trichosurus, major connections to the SG region from the superior colliculus have also been reported, although the laminar origin of these inputs is not definite. (Trichosurus, Rockel et al 1972; Didelphis, Martin 1969, Morest 1965a, Rafols and Matzke 1970; hedgehog and prosimian (Galago), Harting et al 1972).

(ii) CORTICAL RELATIONSHIPS

A number of studies in the cat and monkeys have shown that the SG region projects to insular cortex, with additional projections in the cat to areas medially and caudally adjacent to the principal auditory areas (cat, Graybiel 1973, Heath and Jones 1971, Jones and Leavitt 1973, Niimi and Matsuoka 1979, Winer et al 1977; monkeys, Burton and Jones 1976, Kasdon and Jacobson 1978).

In Trichosurus SG shows a somewhat different distribution of cortical projections, with major inputs to the auditory cortex, overlapping the projections of the medial geniculate nucleus, as well as to adjacent parts of the posterior parietal area (Aitkin and Gates 1983, Neylon and Haight 1983 and see fig 14b).

Examination of the data presented in a number of retrograde degeneration and tracer studies in Didelphis, in which SG has been included within a larger region designated as 'posterior nucleus', suggests that the nucleus may project to temporal cortex, which would indicate a similar arrangement to that seen in Trichosurus (Coleman et al 1977, Diamond and Utley 1963, Donoghue and Ebner 1981a, Pubols 1968).

(iii) FUNCTIONAL CONSIDERATIONS

The functional role or roles of SG are unclear, though some general statements can be made. The main input connections to the region probably originate from the deeper layers of the superior colliculus, which in turn have been shown to receive connections from somesthetic and auditory pathways, as well as from other visual centres (Didelphis, Hazlett et al 1972; Trichosurus, Haight et al 1980, Rockel et al 1972; hedgehog, Jane and Schroeder 1971; tree shrew, Schroeder and Jane

1971; cat, Edwards et al 1979, Gordon 1973, Moore and Goldberg 1963; monkey, Cyanader and Berman 1972, and see Mehler 1969 for information on Didelphis, rat, cat and monkey). Neurons within the cortical projection field of SG in cats and monkeys have been shown to respond to visual, auditory and somesthetic stimuli (Loe and Benevento 1969, Sudanakov et al 1971, Robinson and Burton 1980). SG may then act as a relay for multimodal sensory information from the deeper collicular layers, to regions of cortex adjacent to, or slightly overlapping, the visual, auditory and somesthetic areas. In Trichosurus SG is clearly more strongly linked with the auditory cortex than in the cat and monkeys, but whether this is a general feature of marsupials or a peculiarity of this, and possibly closely related species, remains to be seen.

(c) EXTRAGENICULATE NUCLEUS

Nothing is known of the afferent connections of the extrageniculate nucleus (EG) in Trichosurus and Dasyurus, these nuclei having been identified initially on the basis of their distinctive cortical projections, which terminate in the medial margin of the parietofrontal area (Haight and Neylon 1981b, Haight et al 1983 and see fig 15). In Trichosurus this region of cortex receives caudal body and hindlimb somesthetic projections (Haight and Weller 1973).

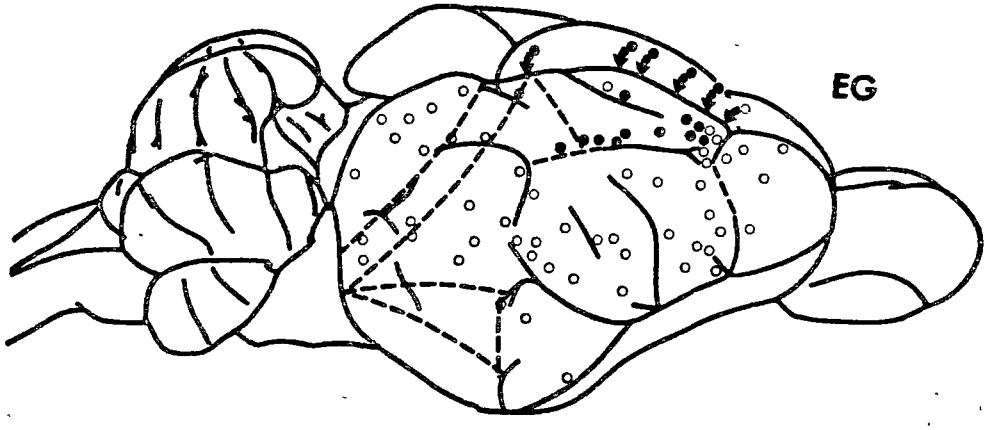


Figure 15

Cortical HRP injections in Trichosurus which produced retrograde labelling in the extrageniculate nucleus (closed circles).

Feldman and Kruger (1980) recently identified a cell group in the rat with very similar positional relationships to EG. They showed that this region, which they termed 'intermediate geniculate nucleus', or IG, receives a major projection from the dorsal column nuclei. Their findings, together with our own in the two marsupial species, strongly suggest that EG and IG are somesthetic relay centres. concerned primarily with body and hindlimb sensation. As stated in the descriptions of nuclear structure, in Trichosurus and Dasyurus the impression one gains of EG, particularly in horizonal sections, is that it comprises a lamina of VP cells largely, but incompletely separated from lateral VPL by fibres of the medial lemniscus and by the intervention of the rostral pole of the medial geniculate nucleus.

Whether EG can in fact be considered as a segment of VPL, isolated from the remainder of the nucleus during development of the thalamus, remains to be seen, however the nature of the input connections of the rat IG, and the distribution of the cortical projections of the Trichosurus and Dasyurus EG would suggest that such speculation is not unreasonable.

(d) SUBPARAFASCICULAR NUCLEUS

In their examination of thalamic input connections in Trichosurus, Rockel et al (1972) included the caudal part of the subparafascicular nucleus (SPF) in their 'parageniculate' (after Dennis and Kerr 1961) component of the posterior nuclear complex, or Pop. Only the dorsal portion of their Pop, however, was found to receive somesthetic pathway projections, and, as we have indicated, (Neylon and Haight 1983), this region is more appropriately considered as part of the posterior nucleus. The input connections of SPF proper remain unknown. In our examinations of thalamocortical projections in Trichosurus we found no evidence for projections to neocortex from SPF (Neylon and Haight 1983).

Only very limited information is available on connections of this centre in other species. Dong et al (1978) reported in the cat that neurons in rostral SPF respond to noxious stimuli, possibly via a spinothalamic pathway. Mehler (1980) has shown that the nucleus has significant projections to the amygdala in monkeys, which would suggest some role in limbic system functions.

SUMMARY AND CONCLUDING STATEMENTS

Lende's (1963 a,b,c) electrophysiological mapping studies of the neocortex in the Virginia opossum *Didelphis virginiana*, and a wallaby *Macropus (= Thylogale) eugenii*, firmly established the notion of a somatic sensory motor cortical 'amalgam' in marsupials. In comparing his findings with those of similar studies in other mammals, Lende (1969) concluded that this condition constituted a primitive level of organisation, while separation of cortical somatic sensory and motor functions was a characteristic of more advanced species. Subsequent research has continued to support the central theme of this concept of cortical evolution, and has confirmed the original findings in *Didelphis*. Rather unfortunate legacies of Lende's work, however, were the general impressions that central nervous system organisation in all marsupials had remained at a primitive *Didelphis*-like stage of development, and that this species could be considered as representative of the group as a whole.

The present thesis has provided an overwhelming body of evidence to dispel such impressions. Comparisons of the cytoarchitecture, afferent connections and cortical relationships of the thalami of *Didelphis* and other American opossums, and of representative Australian

marsupials, reveals many fundamental similarities among the various forms, but also a number of important differences. In addition, some features in particular Australian species indicate considerable progress from the Didelphis level of development, and convergence upon the more elaborate organisational plans seen in several placental lines.

Examples of important interspecies differences among marsupials include the distinctions between Didelphis and the Australian diprotodont species Trichosurus, in the patterns of subcortical afferent and cortical connections of the lateroposterior nucleus, and in the cortical relationships of the dorsal lateral geniculate, anteromedial and mediodorsal nuclei, and some elements of the central intralaminar complex. Another Australian marsupial, the polyprotodont Dasyurus, differs, probably from Didelphis, and definitely from Trichosurus, in having strong cortical projections from the interanterodorsal nucleus.

In some other cases where it has been possible to compare more than two representative marsupial species, variations in thalamic organisation can be seen to be related to particular groupings of animals, or to follow trends across the available samples.

For instance, there is a clear Australian American

dichotomy between Trichosurus and Dasyurus on the one hand, and Didelphis on the other, in the cellular parcellation of the lateral nuclei. A 'geographical' distinction can also be made between these animals in the overall organisation of the main ventral tier nuclei, although Dasyurus does share some features with Didelphis.

A division is apparent between the polyprotodont, and most of the diprotodont species examined so far, with respect to the complexity of the cytoarchitecture and retinal connection patterns of the dorsal lateral geniculate nucleus. Similarly, polyprotodonts and some less advanced diprotodonts differ from advanced diprotodonts in terms of the presence or otherwise of a clearly delineated submedius nucleus, or alternately of a prominent caudal extension of the anteromedial nucleus.

In the three species in which the cytoarchitecture of the midline and central intralaminar nuclei has been examined, the greatest degree of differentiation of these nuclei is evident in Didelphis, and the least in Trichosurus, with Dasyurus exhibiting an intermediate arrangement.

Serological evidence indicates that diprotodont

marsupials have diverged considerably from the stem polyprotodont line, as represented by the didelphids, and that this divergence probably began soon after the separation of the Australian and American populations. On the other hand, Australian polyprotodonts, which show close serological affinities to diprotodonts, have retained a number of morphological characteristics in common with the American forms (see Kirsch 1977). It is not surprising, therefore, to find that representative didelphid and diprotodont species such as Didelphis and Trichosurus show a number of important differences in central nervous system organisation, while representative Australian polyprotodonts, such as Dasyurus, show certain didelphid, or alternately diprotodont characteristics, or in some cases, intermediate arrangements.

That some of the departures from the didelphid organisation seen in Australian marsupials represent a more advanced level of development, is suggested by certain parallels with more highly evolved placental species.

Firstly, there is the high degree of differentiation of the main ventral tier nuclei in Trichosurus and Dasyurus. More importantly, the cortical projection fields of the ventroposterior (somesthetic) and ventrolateral (cerebellar motor) nuclei show

significant separation in these animals, in contrast to their extensive overlap in Didelphis. This corresponds to electrophysiological findings related to the degree of overlap of the somatosensory and motor cortical areas in these animals. It would seem likely that, despite Lende's (1963c) contrary finding in a wallaby, a degree of functional separation is probably present in many, and perhaps all Australian marsupials. These animals may then be considered to show the same evolutionary trend towards cortical functional separation that is apparent in 'higher' placentals.

The principal thalamic visual centres, the dorsal lateral geniculate and lateroposterior nuclei, exhibit complexities of organisation in some diprotodonts which are similar to those seen in the cat and primates. The parallels apparent between such distantly related species as Trichosurus and the cat in the connections of these centres are especially intriguing. In particular, geniculocortical projections in both of these animals show important, and strikingly similar, departures from the general mammalian arrangement.

And finally, the relatively extensive cortical projection field of the mediodorsal nucleus (prefrontal area) in Trichosurus, compared to that in Didelphis and even in some non primate placentals, is another

instance where an Australian marsupial shows strong indications of convergence towards an advanced placental type of organisation.

In comparing thalamic organisation in marsupial and placental mammals, one cannot help but be impressed by the many basic similarities within and between the two groups. In only relatively few cases are there difficulties in recognising regions which are clearly equivalent in different animals, in terms of position, and the principal sources and general distributions of afferent and efferent projections.

Broadly speaking, the connections of particular regions follow, with occasional notable exceptions, what apparently constitute common organisational plans. Where species differences do occur, and these in some cases are quite significant, they can usually be regarded as variations on general themes, rather than total departures from such themes.

Variations relate mostly to points of detail in the distributions of the major input and/or output connections of particular centres, such as the lateroposterior-pulvinar complex. Occasionally one finds a situation where particular connections which are present in many species, may be absent in a few. The apparent lack of projections from the posterior

nucleus to somatic sensory cortex in advanced primates is such a case. Conversely, certain centres in some species may have connections additional to those found in the majority of animals. Examples of this are seen in the cortical relationships of the dorsal lateral geniculate nucleus in Trichosurus and the cat, and of the ventroanterior and suprageniculate nuclei in Trichosurus.

Probably the most fundamental variations in both marsupials and placentals are found in the organisations of the rostral ventral tier and central intralaminar nuclei.

Some differences in the afferent and efferent connections of the rostral ventral tier nuclei (ventroantero-ventrolateral [VA-VL] complex and ventromedial nucleus, or possible equivalent) are sufficiently marked as to make detailed interspecies comparisons difficult. Added to this are such oddities as projections in the cat and in Trichosurus from parts of VA-VL, which is generally recognised as constituting the principal motor nuclear complex of the thalamus, to areas of parietal cortex with mainly somatosensory function. Some rather basic distinctions between mammals concern the varying degrees of convergence of the cortical projections of VA-VL with those of the

ventroposterior nuclei, with corresponding variations in the extent of cortical motor and sensory functional overlap. In addition, the appearance of two possible alternative body representation patterns in the primary motor cortex is presumably reflected by differing arrangements of VA-VL - cortical interrelationships.

Ulinski (1983) has suggested that regions of the thalamus and pallium primarily concerned with motor functions probably appeared only relatively recently in evolutionary terms. These centres, together with some of the other main components of the rather elaborate mammalian motor control systems, may have developed in conjunction with the major modifications in movement patterns and in skeletal structures involved in locomotion and feeding that occurred during the reptile mammal transition. One could speculate, then,that early mammals may still have been experimenting with alternate arrangements of connections between motor centres around the time that the main lineages began to separate. This could have given rise to a number of different possible lines of development, resulting in some of the more important organisational variations evident among present day forms.

A similar argument could be put forward to explain some

of the more pronounced interspecies differences in the organisation of the central intralaminar nuclear group. These include such things as, the apparently unique cortical relationships of some divisions of this group in individual marsupial species, and the appearance in only the cat and primates of a distinct centromedian nucleus, with its strong interrelationships with the motor cortex. The central intralaminar nuclei, like the principal motor thalamic nuclei, (with which they share certain major input connections) may also be very recent innovations in central nervous system evolution. These centres cannot be identified in monotremes, nor with any degree of certainty in non mammals (Ulinski 1983).

Most other parts of the thalamus appear to show somewhat greater consistency of organisation in both marsupials and placentals. Where important variations do occur, as for example in the connections of the main visual relay centres, and in the mediodorsal nucleus-prefrontal cortex system, these mostly concern points of detail, or differences in complexity.

The relative uniformity in connective relationships among some of the forebrain centres involved in sensory and 'limbic' system functions in mammals may be a reflection of the fact that regions with rather similar

functions and connections appear to have been present, though not necessarily in the same form, from early stages of tetrapod evolution (Ulinski 1983). The development of mammalian sensory and limbic system circuitry in the forebrain may then have involved, in part at least, modification of previously existing thalamic and telencephalic structures and connections, rather than the setting up of entirely new organisational frameworks.

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